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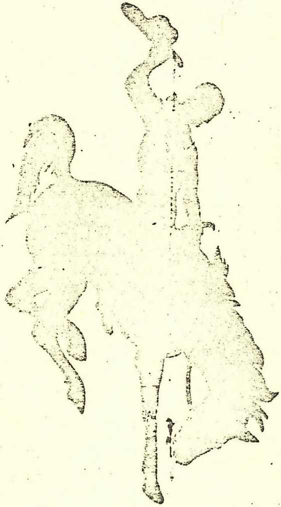

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CORRECTIONS

Page iv - ADD:

Rick Seegmiller
Ecological Overlap Between Feral Burros and Desert Bighorn: A Literature Review (Abstract) 236

Page 99 - AUTHORS AND THEIR RESPECTIVE UNIVERSITIES SHOULD READ:

Rebecca Rudman
Department of Zoology, University of Oklahoma, Norman

Ellen Haag
New York State Veterinary College, Cornell University, Ithaca

Dr. Katherine Albro Houpt
Department of Physiology, New York State Veterinary College, Cornell University, Ithaca

ACKNOWLEDGEMENTS

Early in 1979 we heard that Dr. Hans Klingel was going to be near Laramie in September of that year. Since three of my students and I had been engaged in a major research project on feral horses for the previous three years, I wanted to have Klingel come and talk at the University of Wyoming. The concept snowballed, and soon we had an international conference on our hands, with little or no funding. Thanks to the efforts of Charles Cooper and Kim Carroll of the UW Office of Conferences and Institutes, the conference did take form. The tireless assistance of my students, Rick Miller and Lee Boyd, and other students of the Department of Zoology and Physiology helped the conference to run quite smoothly.

During the meetings I asked that manuscripts of talks be submitted within one month. However, they continued to dribble in through January 1980. After further delay, my wife took over the editing responsibilities, and it is thanks to her that this volume actually appears. My thanks are also due Ruby Sanchez, Pat Beintma, and Andrea Denny for manuscript work.

R.H. Denniston
R. H. Denniston, Ph. D.
Professor of Zoology
Conference Coordinator

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Movements and Home Ranges of Feral Burros on the Tonto Plateau, Grand Canyon National Park

James E. Walters
Resource Management Specialist, Grand Canyon National Park

Abstract

Between September 1977 and May 1979, the movements of feral burros on the Tonto Plateau have been monitored using colored collars and radio transmitting equipment. The data from six radio collars and 32 color coded nylon collars have been plotted and patterns of movements and home ranges have been established for the Tonto Plateau herd. These data demonstrate the continual use of major side canyons as year-around habitation sites for burros within the Inner Canyon of the park. Except for young male burros there is relatively little lateral movement on the Tonto Plateau by this herd.

Seasonal Home Ranges and Activity Patterns of Feral Assateague Island Ponies

Stam. M. Zervanos
The Pennsylvania State University, Berks, Reading

Ronald R. Keiper
The Pennsylvania State University, Mont Alto

Abstract

The seasonal home range sizes and activity patterns of feral ponies occupying Assateague Island National Seashore were studied as part of an overall evaluation of this equid's impact on the island environment. The report is based on data collected over the past two years, using long-range telemetry observations on six pony herds.

It was determined that in summer the herd's average home range size was 6.48 km^2 and home range density averaged 1.99 ponies/ km^2. In winter a smaller average home range size of 4.32 km^2 was observed and the average home range density was 2.53 ponies/ km^2.

Daily herd movement patterns were also more restricted in winter than in summer. Daily herd summer movement exhibited a pattern of grazing on the dunes during the early morning hours and then moving toward the bay and into the marshes by late afternoon. This pattern was not observed during the winter months, when the herds would graze a given habitat throughout the entire day.

In addition, habitat utilization exhibited a seasonal pattern. In summer the ponies spent an average of 18.2% of their time grazing the dunes, while utilizing the inter-dune habitats 19.1% of the time and the marshes 46.9% of the time. In winter, however, the ponies utilized the dunes 25.8% of the time, the inter-dune habitat 34.6% of the time and the marshes 39.8% of the time.

Individual herd variations in these parameters appear to be related to herd size and habitat diversity within each herd's home range.

Introduction

Although the feral ponies inhabiting Assateague Island have received much public notoriety, surprisingly little is known about their actual biology. Recently, Keiper (1976 and 1977) has made some behavioral observations on their social structure and population dynamics. However, much information is still unavailable, particularly the factors influencing their home range and movement patterns.

There are currently six herds occupying the Maryland portion of the island. These herds have been left relatively undisturbed since 1965 when a fence was built at the Maryland-Virginia border, separating the Virginia herds (which are annually rounded up and the foals sold) from the Maryland herds. The six Maryland herds are distributed in very definable home ranges, starting from the Maryland-Virginia border northward to the northern tip of Assateague, a distance of 32 km. Because there is considerable habitat variation both within and among the six herd home ranges, an effort was undertaken to determine the environmental factors influencing the home range size and movement patterns of the ponies.

Of special interest here was how the home range size is influenced by animal herd size and the productivity of the habitat. McNab (1963) and more recently Harestad and Bunnell (1979) have demonstrated empirically that such a relationship might exist in mammals. Thus, a concentrated effort was made to evaluate herd size and forage availability as major factors influencing home range and movement patterns.

Methods

The study was conducted on the Maryland portion of Assateague Island, a 59-km-long barrier island paralleling the Atlantic coasts of Maryland and Virginia. This portion encompasses 8,538 acres and includes Assateague National Seashore. Sixty-four feral ponies (Equus caballus) occupy this area and lead a totally wild existence with little interference from man.

Currently, the ponies are distributed among seven herds, including one bachelor herd and a few solitary individuals. However, the present study concentrated on the six typical herds, each led by a single stallion. They inhabit very definable home areas, splitting the island into six sections. Starting from the Maryland-Virginia border and proceeding northward the herds have been identified as L-, N-, T-, K-, J-, and M- herds.

Telemetry System

Radio-telemetry was used to facilitate data collection on herd location and movement. The telemetry system (Model TTR-1) was manufactured by Telonics, Inc. of Mesa, Arizona. It included ten pulsing transmitters (VHF band) with a range of 1 to 1.5 miles and a life expectancy of 24 to 36 months. The transmitters were urethane encapsulated and attached to the ponies on a lightweight, color-coded, butyl-rubber collar. Tracking was accomplished using a directional antenna and a 10-channel portable receiver.

The radio collars were attached to the ponies by one of two methods. Method one involved tranquilization by means of an intra-muscular injection of 2.5 mg M99 (Etorphine hydrochloride) mixed with 250 mg Rompun (Xylazine) administered by tranquilizer darts shot from a Cap-Chur gun. After attaching the telemetry collar an intravenous injection of M50-50 (diprenophine) was administered to counteract the effects of M99. This procedure was used on 3 June 1978 with limited success. Due to some adverse reactions to the drugging procedure only two collars were attached by this method.

Method two consisted of identifying the tamest pony in a herd and then feeding and occupying it with an apple while the collar was attached. The entire procedure took approximately 30 seconds. Seven collars were applied by this method. Attempts by either method to place a telemetry collar on members of M-Herd proved unsuccessful. However, this herd occupies the northern tip of the island, which is sparsely vegetated and thus the herd could be visually located at all times.

Field Observation Methods

Using two observation methods, a total of 969 observation hours were accumulated over both winter and summer periods from 8 June 1978 to 20 August 1979. The first method of observation involved locating a herd by radio telemetry, noting the time, weather conditions, herd location, and plant types being grazed, then moving on to another herd until all of the herds had been observed. The process took from two to four hours and was repeated throughout the day and night. Daily movement patterns could thus be determined. Using this method, 408 hours (location points) of observation were accumulated, consisting of approximately 55 to 70 hours for each of the six major herds.

The second method involved locating a herd by radio telemetry and staying with it as it grazed. These more intense observation periods lasted for up to five hours. A total of 561 hours (approximately 90 hours per herd) of day and night observations were obtained using this method. In addition to location, information on rate of movement, amount and type of grazing, micro-climate conditions, and type of behavioral activity was collected.

Determination of Vegetation Density

To determine the habitat quality of Assateague, not only is information needed about the quantity of food consumed by the ponies, but also data is required as to the density of the foraged vegetation. Information of the vegetative density was collected, utilizing sampling transects that were established at 0.4-mile intervals along the entire length of the Maryland portion of the island. A total of 60 transect locations were established and analyzed.

At each transect location, three different transects were run (dune, inter-dune, and marsh). For the Dune Transect the highest point on the primary dune was determined. Starting at this point, a 100-foot tape was laid in an east-west direction, with 50 feet lying east of the starting point (toward the beach) and 50 feet lying west of the starting location. The Inter-Dune Transect began at the edge of the sand road running the length of the island and ran 100 feet to the east. The Marsh Transect began along the east-west transect line at the point where the low salt-marsh began and ran 50 feet to the west (the length of the transect was reduced due to the uniform nature of the salt-marsh).

For each transect, sampling was conducted at ten-foot intervals along the tape. At each interval a 2-foot by 2-foot wooden frame (1 foot by 1-foot for the marsh) was centered over the tape. All the plants within this sampling area were identified and recorded. The number of forage plants and stems within the sampling area was also recorded. Finally, the average height of randomly selected forage stems was noted.

Results and Discussion

Factors Influencing Habitat Utilization

The utilization of habitats varied between summer and winter seasons and to some degree among the various herds (Table 1). The major habitats utilized were dune, inter-dune, and marsh, with the ponies using these habitats primarily for grazing on American beach grass (*Ammophila breviligulata*), American three-square sedge (*Scirpus americanus*), and marsh cord grass (*Spartina alterniflora*). The utilization of beach and bay areas during the summer occurred primarily as a means of avoiding biting insects. Except for K-Herd, the most utilized summer habitat was the marsh. The greater density and quality of forage vegetation would make the marsh habitat a more efficient grazing area for the ponies and would, therefore, justify its higher utilization. In fact, the larger herds (T- and M-), with greater total herd energy requirements, spent significantly ($p<.05$) more time in the marsh habitats. The apparent atypical observations on K-Herd are related to their frequenting the park's camping areas (which are dune and inter-dune habitats) and feeding not only on the forage vegetation in these areas, but more importantly on handouts and garbage of campers. In addition, since the camping areas are periodically sprayed with insecticides, the problem of biting insects is less severe here.

Winter utilizations exhibited a general pattern of decreased marsh utilization, with increased utilization of dune and inter-dune habitats. Most of the grazing occurred on beach grass along the back dune-inter-dune ecotone. Very little winter grazing occurred on the fore-dune areas. Winter micro-environmental data indicate that the back-dune and inter-dune areas are more protected from the winter climate, particularly wind velocity. There is also a possible correlation between the wind-chill factor and marsh utilization. As the wind-chill factor approached -15°C, there was less probability of ponies utilizing the marsh areas. Thus, the increased utilization of back-dune-inter-dune areas appears to be related to thermoregulatory factors.

Factors Influencing Movement

The factors affecting herd rate of movement appear to be habitat, season, time of day, and herd size (Tables 1 and 2). Since all these factors interact with each other, there is much variation in the observed data. Thus, generalizations can only be made at this time. In addition, since three times as much data were collected during the summer observation periods, there is less variation and more statistical reliability in the summer data. Therefore, as much as possible, the summer data were used in making the following generalizations.

On the average, herds moved at a higher rate in dune habitats as opposed to the inter-dune and marsh areas. Since dune vegetation is sparsely distributed, compared to the marsh and the heavily utilized sections of inter-dune (see Table 4), grazing proceeded at a faster pace on the dunes. It can be stated that the rate of grazing movement varied inversely with the density of the forage vegetation. L-Herd's high rate of movement on the beach habitat (1.48 km/hr) was due to this herd's use of the beach as a major route for movement both within and without its home range.

Seasonal influences were also observed. The average rates of herd movement were significantly lower ($p<.05$) in winter than in summer (Table 2). This was caused by three factors. First, the ponies in winter restricted their grazing to smaller, more protected areas. There was less movement from one area to another in their daily routine. This resulted in less total movement and more intense grazing of a given area. Second, harassment by biting insects in summer increased herd movement in most habitats. Third, the ponies have more difficulty in feeding on the dry, decaying winter plants.

In addition, a general daily pattern in the rate of movement was observed (Table 2). In summer, herds moved more in the early morning hours (0500-1000) compared to the late afternoon and early evening hours (1500-2000). Movement was significantly slower at night. This correlates well with the herds' summer movement patterns of utilizing dune habitats (with faster rate of grazing movement) in the morning hours, and moving into the marshes (with slower rate of grazing movement) by late afternoon. Winter data are more variable, but show a general pattern of increased movement during the 0500 to 1000 and 1500 to 2000 hour periods. This also correlates with the ponies' general winter movement pattern of staying in a given area throughout most of the day, and moving to another area during the early morning or late evening hours.

There also seems to be an inverse relationship between herd size and rate of movement (Table 2, summer data). The larger herds M- and T- have movement rates ranging between 0.20 km/hr and 0.49 km/hr, while the smaller herds range between 0.24 to 0.88 km/hr. (This is excluding K-Herd, which, because of its restriction to the campground area, exhibited an atypical movement pattern.) Large herd size may hinder more rapid movement due to the increased complexity of their grazing and movement processes. In particular these herds utilized the marsh habitat more heavily, and since grazing rate was slower in this habitat, total movement was also slower.

Factors Influencing Home Range Size

For the purpose of this study, home range was defined as the area encompassing 90 percent of the observed locations for each herd. This assumes that 10 percent of the peripheral observations were forays outside the herd's normal home area. This area concept of home range, as opposed to the mathematical center of activity concept (Hayne, 1949), is similar to that suggested by Burt (1943) and that used by Craighead et al. (1973).

Using this method, the home range of each pony herd during the summers of 1978 and 1979 was determined and delineated on maps of the island (Figures 1 and 2). During 1978 only four previously established herds inhabited the Maryland portion of the island. These were L-, N-, T-, and M-herds. J-Herd was newly established during the summer of 1978 and consisted of four individuals occupying a small portion of the island (Figure 1). During 1979 an additional herd was established (K-Herd) and filled the void between T- and J- herds' 1978 home ranges. In the meantime J-Herd expanded its home range. The result was the establishment of six herd home ranges occupying almost the entire Maryland portion of the island. This also resulted in the decreased size of T- and M-herds' home range (Figure 2).

Thus, in a finite area such as that existing on Assateague, the home range size decreased with increased herd numbers. It can be predicted that as more herds are established on Assateague, the home ranges will exhibit further decline in size.

To establish the effect of forage availability (utilizable energy) on home range size, an effort was made to calculate standing forage biomass within each home range. Table 3 summarizes the results of 180 vegetation transects conducted during the summer of 1979. Using computer-assisted infrared aerial photographs of Assateague as reported by Turner (1979), the total area covered by each forage type was estimated for all the home ranges. The total forage biomass was then calculated by multiplying the density of the plants times the dry weight of each plant times times the area covered by each forage type. By adding all the forage biomass values from each habitat, the total home range forage biomass was determined. The dry weight forage biomass ranged from 38.73 x 10^6 kg in L-Herd's home range at the Maryland-Virginia border to 2.72 x 10^6 kg for M-Herd occupying the sparsely vegetated and over-grazed northern tip of the island.

Home range area was determined from aerial photographs of data reported by Turner (1979). Upon first inspection, the home range size (Table 4) does not appear to be related to herd size. M-herd, with the most individuals (18), has the smallest home range of 218.0 hectares, while T-Herd, with 15 individuals, has the largest home range, 948.0 hectares. However, if the available forage biomass per individual is calculated for each herd, a pattern does appear (Table 4). Excluding L- and M-herds, the available forage biomass values per individual are not significantly different among the four herds (N-, J-, K-, T-). A positive correlation (r=.82) does exist between the number of individuals in a herd and the total available forage biomass within the home range. L- and M- herds do not fit this pattern for several possible reasons. L- Herd is less stable than the other herds. Although it was established three years ago, no mare has ever produced a foal. Its members have also separated several times during the two years of observation. In addition, L-Herd, during short periods in the summers of 1978 and 1979, migrated outof its "normal" area of activity northward into the home ranges of N- and T- herds. This activity was restricted to the beach and dune areas and appears to be exploratory in nature. If these exploratory wanderings are ignored, the home range size for 1979 decreases to 506.2 hectares and includes 81 percent of the observed locations. The new available forage biomass per individual would be 2.94×10^6 kg, not significantly different from the other four herds.

M-Herd's small home range size is difficult to explain. Even during 1978, with little competition from any other herd, M-Herd confined itself to the northern tip of the island (Figure 1). However, even though evidence of over-grazing is indicated, the 0.15×10^6 kg of available forage biomass per individual is sufficient energy to maintain the herd. Perhaps their over-utilization of this small area is due to the fact that this area is relatively free of biting insects, a major summer problem for the other herds. Another reason may be that J-Herd's current home range size restricts M-Herd's southern movement and "traps" M-Herd at the northern tip of the island.

Thus, the variation in the data can be explained, and although there is no apparent relationship between home range size and herd size, there is a correlation between total available forage biomass and herd size. This supports the contentions of McNab (1963) and Harestad and Bunnell (1979) that home range area is related empirically to body weight (or, as in this case, total herd size), particularly if available forage energy is considered.

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Table 1 Utilization of habitats in percent of total observation time and herd movements within habitats in km/hr.

Herd		Habitat									
		Beach		Dune		Inter-Dune		Marsh		Bay	
		Winter	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter	Summer
L	Utilization	0	21.9	26.8	29.3	41.3	14.3	31.9	31.5	0	2.9
	Movement	0.16	1.48	0.24	0.90	0.27	0.40	0.14	0.51	--	0.10
N	Utilization	0	3.6	42.1	8.3	42.1	34.5	15.8	40.0	0	13.5
	Movement	--	0.48	0.16	0.82	0.24	0.49	0.64	0.47	--	0.19
T	Utilization	2.9	4.1	29.4	8.2	17.6	17.5	50.0	61.9	0	8.2
	Movement	0.08	0.32	0.31	0.67	0.26	0.27	0.16	0.21	--	0.32
K	Utilization	13.2	0	31.6	65.2	42.1	19.4	13.2	15.4	0	0
	Movement	0.11	--	0.14	0.25	0.19	0.16	0.17	0.26	--	--
J	Utilization	6.3	10.7	6.3	32.1	31.3	14.3	56.3	42.9	0	0
	Movement	0.08	0.21	0.08	0.48	0.08	0.18	0.13	0.72	--	--
M	Utilization	7.4	1.1	48.1	24.1	18.5	17.2	25.9	57.5	0	0
	Movement	0.16	0.16	0.20	0.29	0.28	0.22	0.13	0.39	--	--

Table 2 Herd daily rate of movement. (N.O. = No Observation)

	Average Movement Per Time Period (km/hr.)							
	0500-1000		1000-1500		1500-2000		2000-2400	
Herd	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter
L	0.87	0.37	0.88	0.19	0.59	N. O.	0.29	N. O.
N	0.55	0.24	0.47	0.28	0.56	N. O.	0.28	N. O.
T	0.31	0.26	0.34	0.17	0.20	0.29	0.08	N. O.
K	0.32	0.16	0.26	0.13	0.18	0.24	N. O.	N. O.
J	0.64	0.08	0.56	0.10	0.24	0.22	N. O.	N. O.
M	0.31	0.23	0.49	0.11	0.20	0.32	0.13	N. O.

Table 3 Home range forage biomass, summer 1979 (in kg. dry wt.)

	Dune			Inter-Dune			Marsh			Total
Herd	No. Plt. per m^2	Ave. Plt. Height (cm)	Total Forage Biomass in Home Range	No. Plt. per m^2	Ave. Plt. Height (cm)	Total Forage Biomass in Home Range	No. Plt. per m^2	Ave. Plt. Height (cm)	Total Forage Biomass in Home Range	Home Range Forage Biomass (kg. dry wt.)
L	30.0	33.1	3.10×10^6	28.5	31.1	0.19×10^6	224.9	33.7	35.44×10^6	38.73×10^6
N	32.6	32.2	3.64×10^6	43.33	27.9	0.13×10^6	295.3	31.4	11.99×10^6	15.76×10^6
T	25.5	31.9	4.96×10^6	20.6	29.2	0.12×10^6	271.4	35.1	33.67×10^6	38.75×10^6
K	15.7	30.1	1.56×10^6	20.1	32.4	0.09×10^6	192.6	34.0	8.34×10^6	9.99×10^6
J	12.6	32.9	0.71×10^6	19.04	29.4	0.03×10^6	209.8	31.9	13.84×10^6	14.58×10^6
M	16.7	23.8	0.58×10^6	27.89	24.8	0.01×10^6	198.3	17.9	2.13×10^6	2.72×10^6

Table 4 Home range sizes and herd densities (A = adult, Y = yearling, F = foal)

Herd	Number of Individuals						Home Range Size (ha)		Home Range Density ha/individual		Available Forage Biomass in kg dry wt/individual	
	1978			1979			1978	1979	1978	1979	1978	1979
	A	Y	F	A	Y	F						
L	6	2	0	7	0	0	822.4	824.0	102.8	117.7	4.83×10^6	5.53×10^6
N	4	2	2	4	1	2	408.4	445.2	51.0	63.6	1.81×10^6	2.25×10^6
T	7	3	5	9	4	2	1142.8	948.0	76.2	63.2	3.11×10^6	2.58×10^6
K	-	-	-	3	2	0	---	456.4	---	91.3	---	2.00×10^6
J	3	1	0	5	1	1	270.4	448.8	67.6	64.1	2.19×10^6	2.08×10^6
M	8	3	6	9	6	3	265.6	218.0	15.6	12.1	0.19×10^6	0.15×10^6

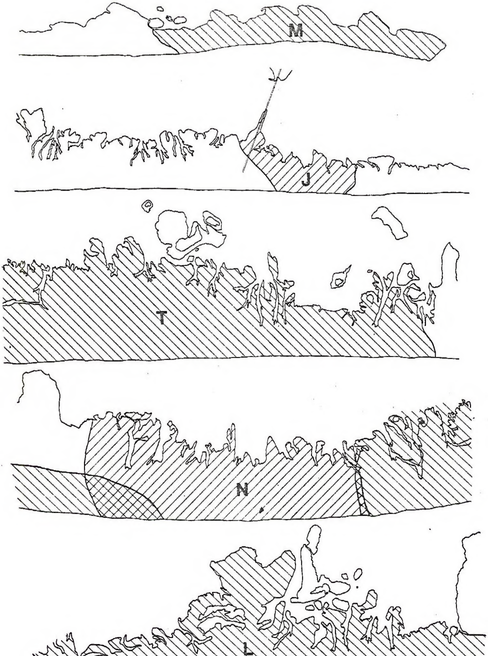

Figure 1. Home range sizes for L-, N-, T-, J-, and M-herds on the Maryland portion of Assateague Island during the summer of 1978.

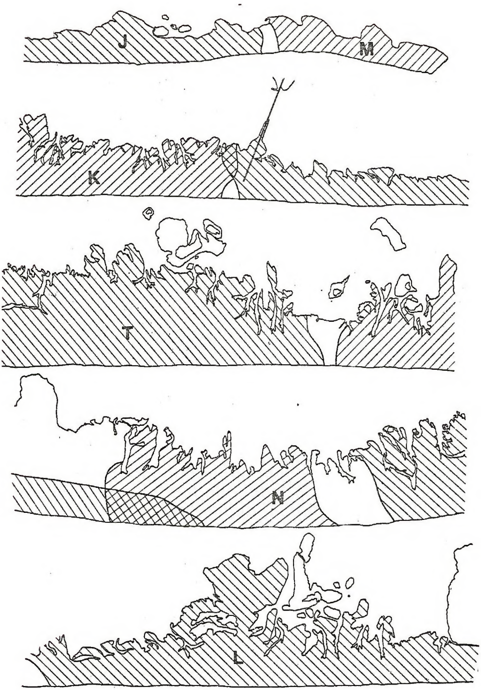

Figure 2. Home range sizes for L-, N-, T-, K-, J-, and M-herds on the Maryland portion of Assateague Island during the summer of 1979.

Summer Diets of Feral Burros (Equus asinus) in Grand Canyon National Park, Arizona

James W. Jordan, George A. Ruffner, Steven W. Carothers, and Arthur M. Phillips, III
Harold S. Colton Research Center, Museum of Northern Arizona, Flagstaff

Abstract

Summer diets of 63 burros (*Equus asinus*) from two study areas in Grand Canyon were analyzed with respect to the availability of forage resources. Bush muhly (*Muhlenbergia porteri*), big galleta (*Hilaria rigida*), and three-awn (*Aristida* spp.) comprised 43.9% of the diet of burros inhabiting the Bedrock Canyon study area, while mesquite (*Prosopis juliflora*), six-weeks fescue (*Festuca octoflora*), and catclaw (*Acacia greggii*) made up 52.0% of the diet of burros occupying the Lower Canyon study area. Several heavily utilized plant species, particularly perennial grasses, were relatively rare within the study areas. Burros are able to forage on a wide variety of plant species, but are highly selective when preferred foods are available.

Introduction

The burro (*Equus asinus*), a native of northeast Africa, is believed to have been introduced into Grand Canyon by 19th century prospectors (McKnight, 1958; Carothers et al., 1976). Originally used as pack animals, burros probably became feral during the early 20th century, a period during which Grand Canyon mining and prospecting activities were subsiding. Habitat relationships of this equine in the Southwest have been addressed by several researchers (Carothers et al., 1976; Woodward and Ohmart, 1976; Hanley and Brady, 1977) who concluded that burros alter the ecology of North American desert communities.

Since the burro has apparently become an established component of the large herbivore fauna of the southwestern United States, an understanding of the life history and ecology of this species is a prerequisite to its proper management. Several previous studies have examined burro diets (McMichael, 1964; Hansen and Martin, 1973; Woodward and Ohmart, 1976), but little information is available regarding the diets of burros in relation to the availability of forage. Qualitative observations of Woodward and Ohmart (1976) indicate that the importance of several plant taxa in burro diets coincides with the periods during which particular plants are most abundant. The objective of this study is to determine the summer diets of burros in two habitat types in relation to available forage resources.

Description of Study Areas

The study areas are located along the north side of the Colorado River, within the Inner Gorge of Grand Canyon National Park, Arizona.

Burros were collected from the vicinity of Bedrock Canyon (Township 33N, Range 2W, to Township 34N, Range 2W) and from the area between Parashont Canyon and Fall Canyon (Township 31N, Range 10W, to Township 29N, Range 10W). The latter region is referred to as the Lower Canyon area. The terrain of both study areas is diverse, varying from sheer cliffs and steep talus hillsides to gentle sloping alluvial fans. Elevations range from 610 to 1524 meters.

The Bedrock Canyon study area is located within the Mohave desert scrub vegetative community (Brown and Lowe, 1974). Characteristic plant species include brittlebush (*Encelia farinosa*), red brome (*Bromus rubens*), fourwing saltbush (*Atriplex canescens*), desert Indian-wheat (*Plantago insularis*), and joint-fir (*Ephedra nevadensis*). Burros are largely confined to the desert scrub community by local topography. There is poor access to the Colorado River and the associated riparian community. Forage resources in the riparian community are limited. Although burros do occasionally water at the river, they rely heavily on seeps and springs in tributary canyons.

In the Lower Canyon study area, burros occupy both the Mohave desert scrub community and a riparian community adjacent to the Colorado River. Typical flora of the desert scrub community includes six-weeks fescue (*Festuca octoflora*), desert Indian-wheat, pepperweed (*Lepidium latipes*), creosote-bush (*Larrea tridentata*), and ocotillo (*Fouquieria splendens*). Dominant plant species of the riparian community are mesquite (*Prosopis juliflora*), creosote-bush, catclaw (*Acacia greggii*), and gray thorn (*Condalia lycioides*). Burros in the Lower Canyon study area have free access to both the desert scrub and riparian communities, and forage resources are abundant in the riparian community. With the onset of winter and spring rains (December-April), burros may range away from the river. During the rest of the year they water, almost exclusively, at the river and depend on the riparian vegetation for forage and shade.

Methods

Eighteen burros were collected during July 1976 from the Bedrock Canyon study area. During August, 19 burros were collected within the Lower Canyon study area. This area was visited again in September, when 26 additional burros were collected.

Approximately 500 cc of well-mixed stomach contents were removed in the field from each specimen and preserved in a 10% formalin solution. Five microscope slides were prepared from each stomach sample using techniques described by Reichman (1975). Twenty non-overlapping fields (100 x) were observed on each slide. A total of 100 fields were observed from each stomach sample. Hansson (1970) and Flinders and Hansen (1972) suggest that 100 fields are sufficient to include rare items. Identifiable items in each field were recorded in terms of relative frequency (relative frequency = number of points of occurrence of one item/number of points of occurrence of all items). Relative frequency was converted to relative density using a table developed by Fracker and Brischle (1944). Sparks and Malechek (1968) have verified the accuracy of this technique. Identification of dietary items was based on comparisons with reference slides prepared from plant species collected in the study areas.

To determine the vegetation composition of the study areas, a minimum of two 100-meter transects were run in each vegetation type during September 1976. Two hundred meters of transect were sampled in the desert scrub community at Bedrock Canyon and in the riparian community of the Lower Canyon area. Three hundred meters of transect were sampled in the desert scrub community of the Lower Canyon. Perennial plants were counted in circular plots 25 m^2, set up at four locations along each transect and encompassing a total area of 100 m^2 per transect. Annual vegetation was analyzed using 1 m^2 plots that were established at 10 m intervals along each transect, for a total of 10 m^2 per transect. Density was determined by counting the number of individuals of each species falling within the respective plots.

Results and Discussion

In the Bedrock Canyon study area, grasses formed 47.8% of the July burro diet, while forbs and browse constituted 17.4% and 31.8% of the diet, respectively. Bush muhly (Muhlenbergia porteri), big galleta (Hilaria rigida), three-awn (Aristida spp.), crypthantha (Cryptantha sp.), catclaw, Anderson wolfberry (Lycium andersonii), white bur-sage (Ambrosia dumosa), and desert Indian-wheat comprised 76.6% of the diet (Table 1).

Browse made up 48.7% and grasses 34.4% of the August diet of burros inhabiting the Lower Canyon study area. Forbs comprised 15.2% of the diet. Principal food items included six-weeks fescue, mesquite, catclaw, trailing four-o'clock (Allionia incarnata), big galleta, globemallow (Sphaerolcea grossulariaefolia), and white bur-sage, which comprised 75.6% of the August burro diet (Table 1).

The September diet of burros inhabiting the Lower Canyon study area included 64.2% browse, 23.3% grasses, and 10.1% forbs. The seven most common dietary items (mesquite, six-weeks fescue, catclaw, white bur-sage, trailing four-o'clock, beavertail or prickly pear cactus--Opuntia spp. - and big galleta) comprised 76.2% of the September burro diet (Table 1).

Utilization of available flora was not uniform, as burros foraged extensively on several relatively uncommon plant species, while little use was made of many dominant plants. On vegetation transects in the Bedrock Canyon study area, red brome, brittlebush, gilia (Gilia sp.) and fourwing saltbush constituted 69.9% of the vegetation available to burros (Table 2), but only red brome was found in the July burro diet and represented 0.1% of the forage consumed (Table 1). In the Lower Canyon study area, six-weeks fescue, red brome, desert Indian-wheat, and pepperweed comprised 64.1% of the available vegetation within the Mohave desert scrub community, while mesquite, red brome, creosote-bush and catclaw formed 86.3% of the plant resources within the riparian community (Table 2). Six-weeks fescue, mesquite, and catclaw were the only dominant species heavily utilized by burros in the Lower Canyon study area (Table 1).

Eleven species of plants not encountered on vegetation transects in the Bedrock Canyon study area constituted 62.4% of the July diet of burros (Tables 1 and 2). In the Lower Canyon study area, 12 species of plants not encountered on the transects comprised 26.9% and 22.6% of the August and September burro diets, respectively (Tables 1 and 2). The most important species in this category, with respect to their relative densities in the diets, were bush muhly, cryptantha, white bur-sage, and

Anderson wolfberry in the Bedrock Canyon study area, and big galleta, white bur-sage, camel-thorn (Alhagi camelorum) and globe-mallow in the Lower Canyon study area. The failure to find some species on the transects that were present in the diets may be due to their rare occurrence. For example, catclaw and Anderson wolfberry in the Bedrock Canyon study area are found only on the margins of ephemeral drainages. Our vegetation transects did not cross this habitat. Heavy utilization of relatively uncommon or restricted plant species demonstrates a high degree of dietary selectivity by burros.

We did not identify brittlebush in the July or September diets of burros,and found only trace amounts (0.3%) in the August burro diet. McMichael (1964) reported that this plant formed 12% of the summer diet of burros inhabiting the Black Mountains of northwestern Arizona. Creosote-bush, a common plant on the Lower Canyon study area, was not browsed during August or September. Woodward and Ohmart (1976) found that creosote-bush constituted 3.6% of the September diet of burros within the Chemehuevi Mountains of southeastern California. These findings indicate the regional variability of burro diets. Janis (1976) has shown that while horses and ruminants do equally well on diets which typically have a low fiber to protein ratio, horses are better adapted to digest forage with a high fiber to protein ratio. As the fiber content of forage increases, plants remain in the rumen longer and intake is reduced (Janis,1976). Thus, regional variation in diets of burros may reflect their ability to digest plants with either low or high fiber to protein ratios. Burros are selective when preferred foods are available, but are also able to forage on a wide range of species.

Burros utilized more grasses than forbs and browse in the Bedrock Canyon study area and more browse than grasses and forbs in the Lower Canyon study area. This variation reflects the absence of mesquite from the Bedrock Canyon study area on the selective foraging of burros on mesquite leaves and ripened pods within the riparian zone of the Lower Canyon study area. Woodward and Ohmart (1976) suggest that increased utilization of mesquite during July and August reflects the concentration of burro activities in the riparian zone during the hottest time of the year and the ripening of the mesquite pods.

Perennial grasses were relatively uncommon on vegetation transects in both study areas, suggesting that the availability of these plants is low. Yet, perennial grasses constituted 38.0%, 10.8% and 9.7% of the July, August,and September burro diets, respectively. Phillips et al. (1977) found perennial grasses to be abundant on the south side of the Colorado River, in areas uninhabited by burros. Big galleta ranked as the dominant perennial plant in Mohave desert scrub communities on the south side of the river. We attribute the reduction of perennial grasses on the north side of the Colorado River to selective grazing by burros.

Hansen and Martin (1973), working in western Grand Canyon, found that perennial grasses were a major component of the diet of burros, making up 53.5% of the annual diet. Weaver (1972) suggested that burros were responsible for the decimation of perennial grasses in Death Valley, California.

Reasons for the selective grazing of perennial grasses by burros are open to conjecture. There may be a relationship between burro dietary preferences and energetics. McKell (1975) noted that mature grasses in the Great Basin of western North America had a greater value of digestible energy (kcal/lb) than did sympatric shrubs or forbs. Further studies of burro energy requirements, energy expenditures during foraging, energy content of forage, and assimilation efficiencies of preferred foods may clarify the role of perennial grasses in burro diets.

Acknowledgements

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Table 1. Monthly percentages of foods in summer diets of feral burros, Grand Canyon National Park, Arizona.[1]

Principal Foods		Bedrock Canyon Study Area - July	Lower Canyon Study Area	
Species	Common Name		August	September
Grasses:				
Aristida spp.	Three-awn	9.5	1.7	2.6
Festuca octoflora	Six-week fescue	---	21.6	10.2
Hilaria rigida	Big galleta	10.9	6.1	4.9
Muhlenbergia porteri	Bush muhly	23.5	---	---
Oryzopsis hymenoides	Indian ricegrass	1.0	0.6	1.1
Sporobolus spp.	Dropseed	2.6	1.8	0.9
Tridens pulchellus	Desert fluffgrass	---	2.3	2.8
Others		0.3	0.3	0.8
Forbs:				
Allionia incarnata	Trailing four-o'clock	---	8.7	6.3
Cryptantha sp.	Cryptantha	7.2	0.5	0.8
Eriogonum spp.	Buckwheat	2.2	0.4	0.3
Melilotus alba	White sweet-clover	---	1.5	1.1
Physalis crassifolia	Ground cherry	1.6	---	---
Plantago insularis	Desert Indian-wheat	5.7	2.5	1.2
Others		0.7	1.6	0.4
Browse:				
Acacia greggii	Catclaw	7.1	14.7	8.7
Agave utahensis	Century-plant	3.0	0.2	1.3
Alhagi camelorum	Camel-thorn	---	3.6	2.1
Ambrosia dumosa	White bur-sage	6.2	4.4	6.5
Ephedra spp.	Jointfir	3.3	1.1	1.6
Fouquieria splendens	Ocotillo	---	0.5	1.8
Lycium andersonii	Anderson wolfberry	6.5	1.2	0.3
Opuntia spp.	Prickly-pear or beavertail cactus	0.1	1.1	6.2
Prosopis juliflora	Mesquite	---	15.5	33.4
Sphaeralcea ambigua	Globe-mallow	---	4.6	1.0
Stephanomeria pauciflora	Wire-lettuce	1.5	---	---
Tamarix pentandra	Salt cedar	3.0	0.8	0.5
Others		1.1	1.0	0.8
Unknowns		4.1	1.8	2.6

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[1] Other genera occurring in diets were: *Andropogon*, *Bromus*, *Aster*, *Porophyllum*, *Aloysia*, *Nolina*, *Cassia*, *Euphorbia*, *Mirabilis*, *Oenothera*, *Pectis*, *Stanleya*, *Atriplex*, *Bebbia*, *Brickellia*, *Encelia*, *Krameria* and *Pluchea*.

TABLE 2. RELATIVE DENSITIES OF MAJOR PLANT SPECIES AVAILABLE TO FERAL BURROS, GRAND CANYON NATIONAL PARK ARIZONA

SPECIES	COMMON NAME	BEDROCK CANYON STUDY AREA	LOWER CANYON STUDY AREA	
		DESERT SCRUB COMMUNITY	DESERT SCRUB COMMUNITY	RIPARIAN COMMUNITY
GRASSES:				
ARISTIDA SP.	THREE-AWN	0.1	---	---
BROMUS RUBENS	RED BROME	59.3	18.9	24.3
FESTUCA OCTOFLORA	SIX-WEEKS FESCUE	---	28.2	---
HILARIA RIGIDA	BIG GALLETA	1.8	---	---
PANICUM CAPILLARE	WITCHGRASS	---	---	3.3
TRIDENS PULCHELLUS	DESERT FLUFFGRASS	0.6	0.1	---
FORBS:				
ALLIONIA INCARNATA	TRAILING FOUR O'CLOCK	---	0.2	0.7
ASTRAGALUS NUTTALLIANUS	MILKVETCH	---	0.7	---
CHORIZANTHE BREVICORNU	CHORIZANTHE	---	1.9	---
CRYPTANTHA SP.	CRYPTANTHA	---	TR.	---
DELPHINIUM SP.	LARKSPUR	---	0.1	---
DESCURAINIA SP.	TANSY-MUSTARD	0.7	0.6	1.8
FILAGO SP.	FILAGO	---	1.5	---
GILIA SP.	GILIA	3.1	2.9	---
LINANTHUS SP.	LINANTHUS	---	0.4	---
LEPIDIUM SP.	PEPPER WEED	---	8.4	---
PECTOCARYA SP.	MOONSEED	---	2.2	---
PLANTAGO INSULARIS	DESERT INDIAN-WHEAT	2.6	8.6	1.5
POLEMONIACEAE	PHLOX	---	0.5	---
POROPHYLLUM GRACILE	PORELEAF	---	0.1	---
STREPTANTHUS SP.	TWISTFLOWER	---	0.4	---
BROWSE:				
ACACIA GREGGII	CATCLAW	---	---	5.9
AGAVE UTAHENSIS	UTAH AGAVE	0.3	---	---
CONDALIA LYCIOIDES	GRAY THORN	---	---	4.1
ECHINOCEREUS ENGELMANNII	HEDGEHOG CACTUS	---	0.2	---
ENCELIA FARINOSA	BRITTLEBUSH	4.8	2.4	---
EPHEDRA NEVADENSIS	JOINT-FIR	2.6	0.4	---
FEROCACTUS ACANTHODES	BARREL CACTUS	1.1	---	---
FOUQUIERIA SPLENDENS	OCOTILLO	---	0.2	---
GUTIERREZIA LUCIDA	STICKY SNAKEWEED	0.6	---	---
HAPLOPAPPUS ACRADENIUS	PALELEAF GOLDENWEED	1.0	---	---
KRAMERIA PARVIFOLIA	RATANY	---	0.2	---
LARREA TRIDENTATA	CREOSOTE-BUSH	---	1.9	14.4
MAMMILLARIA MICROCARPA	MAMMILLARIA	---	TR.	---
OPUNTIA BASILARIS	BEAVERTAIL CACTUS	0.3	1.1	---
OPUNTIA PHAEACANTHA	PRICKLY-PEAR	0.3	---	---
OPUNTIA WHIPPLEI	CHOLLA	---	0.4	---
PROSOPIS JULIFLORA	MESQUITE	---	---	41.7
SPHAERALCEA GROSSULARIAEFOLIA	GLOBE-MALLOW	0.9	---	---
ATRIPLEX CANESCENS	FOURWING SALTBUSH	2.7	---	---
OTHERS:				
CAMISSONIA SP.	FERN	---	0.6	---
TORTULA SP.	CRUSTOSE MOSS	17.1	16.8	2.2

A Comparison of the Social Organization of the Equids

Hans Klingel
Zoologisches Institut, Universität Braunschweig, West Germany

Abstract

The six species of extant equids are remarkably uniform with respect to size, morphology, physiology, general life habits, and behavior. One of the most striking differences concerns social organization, and two distinct types of mating systems have evolved.

Plains zebra, mountain zebra, and horse live in family groups consisting of one stallion, one to several mares and their young. These groups are stable with respect to the adult members who are not closely related to each other. Adolescent mares are abducted by other stallions who thereby start a family or increase the number of their mares. Young stallions leave the family on their own accord. Surplus stallions of all age classes live in bachelor groups which are to some extent stable.

The social units live in large overlapping home ranges whose sizes depend on ecological factors. There is no competition whatsoever for space, i.e., these species are non-territorial. Mating rights are established by the stallions through their presence with the mares, and their position is respected by other stallions. This system breaks down when adolescent mares display the estrous stance, which attracts stallions from the vicinity of the group.

In Grevy's zebra, African wild ass, and Asiatic wild ass, some of the adult stallions are territorial and inside their territories dominant over, and at the same time, tolerant towards all their conspecifics. Mares, foals, and non-territorial stallions live in unstable groups of varying size and composition, and the only permanently stable units are those of mares and their young.

In Grevy's zebra territories are kept, by the same stallions and in the same places, for years, even though they may be abandoned for some time during the height of a dry season.

With the exception of a few small populations, equids live in areas of seasonal or irregular rainfall patterns and they are accordingly forced to migrate.

The non-territorial species move always as complete reproductive units, and they therefore seem to be sociologically well adapted to regular as well as irregular changes of the environment. In contrast to this, the territorial species should be better suited to constant or regularly changing conditions, especially since the strong attachment of the stallions to their territories (as in Grevy's zebra) leads to a segregation of the sexes.

The actual distribution of the various species (with one exception: mountain zebra) is not in accordance with the sociological features, and other adaptations are considered to be decisive for the performance under extreme conditions.

Both types of social organization have evolved from the certainly more primitive system of Eohippus. The various types of social organization of bovids may serve as a model.

Discussion

The six species of extant equids are very similar in their morphological and general physiological features, and they are all members of one genus, Equus. They are predominantly grazers inhabiting mostly open grasslands. Seasonal or irregular rainfall patterns cause the members of all but a few populations to undertake regular or irregular migrations. All equids, even those living in arid habitats, need to drink regularly. Many behavior patterns--mating, mother-offspring, grooming, fighting behaviors--are very similar.

However, there are marked differences in their social organization, where two types can be distinguished. I have been fortunate enough to be able to study, from 1962 to 1973, the life habits of five of the six species in their natural environments: plains zebra (E. quagga, also referred to as E. burchelli) in the Ngorongoro Crater, the Serengeti National Park, and the Rukwa Game Reserve in Tanzania, in Kenya, Rhodesia, Mozambique, South and South-West Africa; Cape mountain zebra in the Mountain Zebra National Park in South Africa; Hartmann's zebra in South-West Africa; Grevy's zebra in northern Kenya; African wild ass in the Danakil Desert of Ethiopia; and Asiatic wild ass in the Badchys Reserve in Turkmenia, USSR (Klingel, 1967, 1968, 1969, 1974, 1977). I include in this overview also the horse (E. przewalskii f. caballus)of which a number of feral populations have been studied in England (Tyler, 1972) and in North America (Feist, 1971; Feist and McCullough, 1976; Berger, 1977; Miller, 1979; Keiper, 1976; Welsh,1973).

Type 1 of the equid social organization is characterized by non-territorial coherent family units and stallion groups and is present in plains zebra, mountain zebra, and horse.

Type 2, characterized by mating territoriality of the stallions, occurs in Grevy's zebra and in African and Asiatic wild asses.

The family groups of Type 1 consist of one stallion, one to several (up to six) mares and their young. Family sizes are different in the various populations, and the maxima are around 16. The family units are permanent associations of the adult members. In 41 plains zebra families (156 adults) only three sociologically caused changes concerning adults took place over two years: two family stallions were replaced, and one mare joined. (Ten more changes were caused by deaths.) Penzhorn (1975), who continued my earlier observations on Cape mountain zebra, found most of my original families six and even eight years later still intact--except for some mortality. All the studies on feral horses indicate a similar stability. Also, in two zebra species, there is little antagonism among stallions for the possession of families, and family groups and bachelor stallions live quite peacefully close together. In feral horses, family stallions are more frequently challenged by other stallions (e.g. Welsh, 1973; Berger, 1977; Miller, 1979), but the duration of their tenure is similar to that of the two zebras.

It is remarkable that, in one feral horse population in the Red Desert of Wyoming, some family groups contained up to three adult stallions (Miller, 1979).

Family stallions may be replaced by stronger ones when they are sick and/or old. In this situation the strong cohesion within the groups is clearly demonstrated: the mares (who are not related!) stay together and are taken over as a whole by the new stallion. This is proof that the mares are not kept together by force, by the stallion. The cohesion is based on individual recognition by visual, acoustical, and chemical cues.

Surplus stallions join up in stallion groups which may also be permanent for years, but not as stable as the family groups. Family stallions are recruited from the stallion groups. Regular changes occur in the families with respect to the subadult animals.

In plains zebra, subadult mares are abducted at age one to two, by other stallions, who are attacked by the family stallion in his vain attempts to keep the mares. In Cape mountain zebra probably the same feature occurs (Penzhorn, 1975), whereas Joubert (1971) reports that young mares are expelled from the family. In the horse, expulsion seems to take place as well, or the young mares just wander off (Welsh, 1973). Subadult stallions leave their families at age one to three and join stallion groups. Both social units,family and stallion groups, live in undefended, overlapping home ranges, i. e., they are not territorial. One feral horse population of Assateague Island, Virginia/Maryland, is unique in this respect, as overlap is minimal and each family group has in fact its exclusive, albeit undefended, home range (Zervanos and Keiper, 1979). Especially plains zebra, who occur in rather large populations, join up to form big herds numbering hundreds and, in the Serengeti, even 10,000 and more individuals. These herds are by no means stable social units, and the discrete families and stallion groups stay intact. This is also the case when large numbers of individuals congregate at water holes, during migration, and flight. No intergroup dominance was observed in such aggregations; however, in feral horse populations where a resource (water) was limited, larger groups were dominant over smaller ones (Berger, 1977; Miller and Denniston, 1979).

In the representatives of the second type of social organization, Grevy's zebra, African and Asiatic wild asses, there are no permanent bonds between any adult individuals. They live in unstable, anonymous associations of varied composition. Stallion groups, mare groups, mare and foal groups, and mixed groups can be distinguished. The only stable units are those of a mare and her offspring. Mating strategy in these species (observations on Asiatic wild ass are still scanty; Klingel, 1977) is the establishing of mating territories by some of the adult stallions (about 25% in Grevy's zebra). This territoriality is unusual, compared to mating territoriality of other ungulates in the following ways:

(1) The territories are extremely large. They measured from 2.5 to 10.5, mean 5.75 km^2, on one of our Grevy's zebra studies in northern Kenya, and were in the order of 20 km^2 in the Danakil (African wild ass) and in Badchys (Asiatic wild ass). These are obviously the largest mating territories known.

(2) The territorial stallions are tolerant towards all conspecifics, and they especially permit other stallions to enter the territory and stay there. However, visiting stallions are subordinate, and the territorial stallion is testing their subordination by driving them short distances within the territory. Fights have been observed to occur, in Grevy's zebra, for the possession of a territory, and among territorial neighbors, in the presence of an estrous mare in the border area.

(3) The territories are marked with dung piles, which--in contrast to general opinion--do not serve to prevent conspecifics from entering, but which seem to be used as orientation marks for the territorial individual himself. Considering the size of the territories and the rather featureless habitat, it seems to be imperative that a territorial animal produces

marks which he can subsequently recognize and which enable him to display the "right" behavior in the "right" place.

Some additional features have been discovered in feral donkeys. In Moehlman's (1974) Death Valley population, multiple matings took place outside the territories, and in spite of continuous fighting among the competitors.

In the Ossabaw Island, Georgia, population, the territorial stallion assisted by his sons, prevents the mares from leaving the territory, and both father and sons have the mating rights (McCort, 1979).

In Grevy's zebra, and probably also in the African and Asiatic wild asses, the territories are permanent institutions, and they are kept for years. However, the territorial individual may leave the territory for short periods to go to a water hole, or even for several months, during severe dry periods (Klingel, 1974).

The existence of two basically different types of social organization in an otherwise homogeneous genus is striking. But it is even more remarkable, when one tries to assess their adaptive significance.

The representatives of Type 2 seem to be adapted sociologically to areas with either constant or regularly changing conditions: the males are permanently territorial, and they have a particularly strong attachment to their territories. However, at least two of the three species, namely Grevy's zebra and the African wild ass, live in deserts and semideserts where rainfall is irregular to unpredictable.

On the other hand, the non-territorial species, which live in permanently reproductive units, seem to be sociologically adapted to any environment, even one with unpredictable rainfall, as they can migrate unrestrictedly. But only one of the three species is in fact a desert animal: Hartmann's zebra, one of the two mountain zebras.

This indicates that the present distribution of the equids is only partly in accordance with their sociological features, and that physiological adaptations to desert conditions are more important than sociological traits.

That this is the case was clearly demonstrated during a drought in the early 1970's in the overlap zone in northern Kenya. Plains zebra were severely reduced in numbers through lack of good water and probably also through starvation, whereas Grevy's zebra suffered only from reduced reproduction. On the other hand, even in years with average rainfall did Grevy's zebra not extend their range. This is probably because under these conditions their performance is inferior to that of the plains zebra.

The apparent paradox of equid distribution may thus have a simple explanation, namely, that the mating territoriality of the Type 2 species evolved under much more regular conditions, and that these species retreated to the arid habitats because they became subjected to competition from the Type 1 species.

Where and when the sociological evolution has taken place is impossible to reconstruct. There is, however, some evidence that all the extant equids evolved as species on the North American continent, and that Grevy's zebra and the African and Asiatic wild asses were the first to cross the Bering Bridge, in the early Pleistocene, whereas the remaining species came to the Old World only during the late Pleistocene. This would explain the much wider range of Grevy's zebra in Africa during the Pleistocene, i. e., before their major competitors, plains and mountain zebra, had arrived. It is feasible that similar situations existed with respect to African and Asiatic wild asses.

Future research should, whenever possible, take into account the problem of interspecific competition. This will be interesting enough in its own right, but the results may also throw some light on the mechanics of equid evolution and lead to a better understanding of their life habits.

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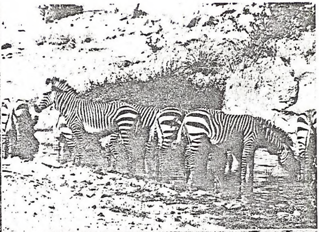
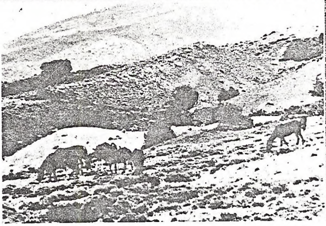
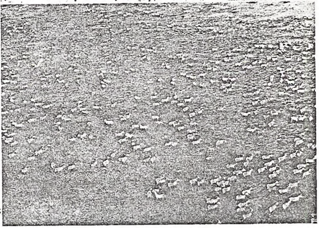






TOP

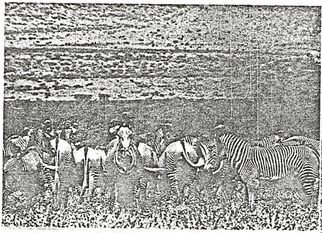
(Left) Plains zebra family group. Mara Reserve, Kenya.

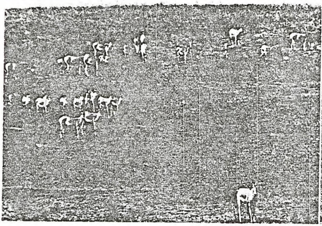
(Right) Hartmann's zebra family group. Etosha National Park, South-West-Africa.

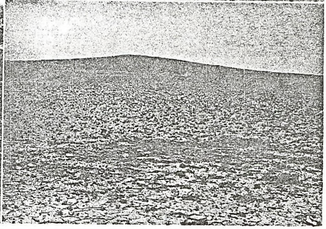
BOTTOM

(Left) Feral horse family group. Pryor Mountains, Montana.
(Photograph: Courtesy of Dr. D. R. McCullough)

(Right) Plains zebra aggregation. Serengeti National Park, Tanzania.







TOP

(Left) Grevy's zebra mixed herd with territorial stallion (right). Il Bonyeki Plains, Kenya.

(Right) African wild ass territorial stallion with mares and foals. Danakil, Ethiopia.

BOTTOM

(Left) Asiatic wild ass territorial stallion with mixed herd. Badchys Reserve, Turkmenia, USSR.

(Right) Dung pile, an orientation mark, African wild ass. Danakil Desert, Ethiopia.

Androgens in Feral Stallions

Marlane Angle, Steve Swain, and J. F. Kirkpatrick
Department of Biological Sciences, Eastern Montana College, Billings

J. W. Turner, Jr.
Department of Physiology, Medical College of Ohio, Toledo

R. M. Kenney
School of Veterinary Medicine, University of Pennsylvania, Kennett Square

V. K. Ganjam
Department of Physiology, School of Veterinary Medicine, Auburn
University, Auburn, Alabama

Abstract

Seasonal and diurnal patterns of 17 beta-hydroxyandrogens and testosterone in feral stallions are reviewed, and new data for two-year-old stallions with descended and undescended testes are presented. Previous work has demonstrated that mature feral stallions (three years or older) have a seasonal pattern of testosterone and total androgen secretion with peak levels occurring in May and a nadir from late September through December. As the blood levels of total androgens increased, the percent which was testosterone also increased. The seasonal pattern was similar to that of Quarter horses. Diurnal patterns indicated peak levels of testosterone at 0800 hrs and the nadir at 2300 hrs. An eight-year-old bachelor stallion which had demonstrated a consistent lack of libido had significantly lower testosterone levels ($P < 0.01$) than harem stallions, suggesting a relationship between plasma testosterone levels and reproductive behavior in feral stallions. The day-time blood levels of testosterone and total 17 beta-hydroxyandrogens were evaluated in two two-year-old stallions which had descended testes and had recently been driven from their respective bands. The same steroids were examined in 19 two-year-old stallions with undescended testes, all of which were permitted to remain with their harem bands. The two-year-old males with descended testes had testosterone concentrations of 1.9 and 4.8 ng/ml with a mean of 3.35 ng/ml, while the 19 two-year-old males with undescended testes had a mean testosterone concentration of 1.14 ± 0.23 ng/ml.

Presently there are an estimated 50,000 to 70,000 feral horses inhabiting the western United States. The herd size increases annually due to the protection afforded by the Wild and Free Roaming Horse and Burro Act of 1971 (P.L. 92-195) and inadequate means of population control. Reversible chemical fertility control, focused upon the stallion, is currently a possibility. The stallion is the target animal, rather than the mare, because of the harem band social structure. Such an approach requires a background study of basic reproductive physiology of the feral stallion.

This paper reviews previous work regarding the plasma levels of 17-beta-hydroxyandrogens and testosterone in feral stallions, and the diurnal variations and seasonal changes of these steroids. Additionally, new data regarding plasma testosterone in feral stallions with descended and undescended testes are presented.

Methods and Materials

Diurnal Study: Four stallions from the Pryor Mountain Wild Horse Range in Montana were captured and confined to a corral several days before blood was collected. On the day of collection, the horses were restrained by halter ropes, to posts on opposite sides of each horse. This permitted the animals some movement but without danger of injuring themselves. The four animals were identified by name: Crooked Creek (CC); Welfare (W); Black (B); and Sorrel (S). These stallions were nine, eight, eight, and six years old respectively, and all were in good physical condition.

Beginning at 1600, 10 ml blood samples were collected hourly, by jugular venipuncture, in heparinized tubes, centrifuged, and the plasma immediately frozen on dry ice.

Seasonal Study: Thirty-four sexually mature (three years of older) stallions were captured on their home range in the Pryor Mountains, during September, October, December, March, May, and July. The animals were brought down by heading and heeling and blood samples were collected by jugular venipuncture. The heparinized blood samples were packed in ice and centrifuged within 24 hrs. of collection.

Immature Stallion Study: Nineteen two-year-old stallions with undescended testes were captured on the Pryor Mountain range. These sexually immature stallions were all permitted, by their respective harem stallions, to remain with their respective harem groups. Two additional two-year-old stallions were captured, which had descended testes and which had been recently driven from their harem groups. Blood samples were collected from all 21 animals as previously described.

Testosterone Assay: Total 17 beta-hydroxyandrogens were extracted from duplicate 0.5 ml plasma samples with three washes of diethyl ether, totalling 10 ml. The ether extracts were washed with two volumes of 0.1 N NaOH to remove estrogens. Testosterone (4-androsten-17 beta-ol-3-one) was separated from other 17 beta-hydroxyandrogens by Sephadex LH-20 column chromatography. The column was 6 mm (I.D.) X 31 cm and the solvent system was reagent grade heptane:chloroform: ethanol:water (50:50:1:saturation). Columns were prepared daily from a solvent-Sephadex slurry and eluted with 100 mls of solvent before use. The testosterone elution profile and percent recovery were established with ^{3}H-testosterone. One ml fractions 31 through 40 yielded 95 ± 2.8 percent (N=10) of the ^{3}H-testosterone.

Ether extracts of the plasma were dried and 1.0 ml of column solvent was added to each tube. Testosterone was collected in elutions 31 through 40, eluates were dried and 2 mls of ether were added and dried. Thin-layer chromatography was used to confirm results obtained with column chromatography. TLC was carried out with precoated silica gel plates (Van Waters Rogers) and petroleum ether:toluene (1:1 by volume) and 85 percent methanol. Identification was made with p-methoxybenzaldehyde (Kodak Chemicals).

Quantitation of plasma testosterone was accomplished by competitive-protein-binding assay described by Ganjam and Amann (1973). The protein-tracer-solution (PTS) consisted of 99.5 mls distilled water, 0.5 mls of third trimester human pregnancy plasma and (1,2,6,7-^{3}H) testosterone (New England Nuclear). The PTS was prepared fresh daily and stored at 5°C for at least one hour before use. The testosterone standard (Steraloids, Pawling, N.Y.) was recrystallized once and stored at 5°C in ethanol at a concentration of 10 ng/ml. Unbound steroid was removed by the addition of 40 mg Florisil (60/100 mesh) and shaking for two minutes. After 15 additional minutes of refrigeration, 0.5 mls of the PTS-testosterone complex was pipetted into 5 mls of toluene base scintillation cocktail (Liquiflor, New England Nuclear). This two-phase system was counted 24 hrs later in a Nuclear Chicago Model 720 LSC. Counting efficiency for tritium was 22 percent.

a) Recovery. Recovery of testosterone after extraction and column chromatography was 91.2 ± 3.7 percent (N=10) as determined by internal standard.
b) Precision. The coefficient of variation was 10.4 percent for 22 duplicate determinations carried out on different days. The inter-assay and intra-assay variation was 12.1 percent and 8.2 percent respectively.
c) Accuracy. Known amounts of testosterone standard (N=25) were assayed. Analysis of variance yielded a correlation coefficient of $r = 0.932$.
d) Specificity. The specificity of this assay is dependent upon the separation of testosterone from other 17 beta-hydroxyandrogens and estrogens (Vermeulin and Verdonck, 1970) and was evaluated by examining the constancy of testosterone standards after chromatography.
e) Sensitivity. Ten distilled water blanks gave an average value of 0.12 ± 0.09 ng/ml. The lowest value for measurable testosterone standards which differed from the blank value ($P < 0.05$) was 0.28 ng/ml.

Statistical Methods: Data were analyzed by analysis of variance and tested for significance with Duncans New Multiple Range Test (Alder and Roessler, 1972).

Results

Diurnal Variation: One of the horses, (S), never adjusted to the restraint and handling procedures. After the tenth hour of sampling this animal was released in order to prevent increased stress and probable death. As a result no data have been included for this horse. None of the remaining three horses showed undue stress; however, (W) remained somewhat aggressive throughout the study.

A definite diurnal variation in plasma testosterone was exhibited by all three stallions. The mean testosterone concentrations reached a nadir of 1.37 ±0.75 ng/ml plasma at 2300 and a peak of 3.48 ± 0.12 ng/ml plasma at 0800. The mean low concentration at 2300 differed significantly ($P < 0.01$) from those at 2300 to midnight and through 0400. The general pattern of testosterone levels indicated an increase beginning in the early morning hours. The testosterone concentrations more or less maintained a plateau during the daylight hours between 0800 and 1800.

Of the three animals, the stud stallion Welfare had the highest mean testosterone concentration for the 24 hrs (3.2 ± 0.7 ng/ml). The stud stallion Crooked Creek had a 24-hr mean testosterone concentration of 2.7 ± 0.6 ng/ml. The bachelor stallion Black had a 24-hr mean testosterone concentration of 1.5 ± 0.9 ng/ml and differed significantly ($P < 0.01$) from both of the stud stallions. At both midnight and 0400 the bachelor stallion's testosterone concentrations were nondetectable (Kirkpatrick et al., 1976).

Seasonal Variation: A clear seasonal variation existed for plasma 17-beta-hydroxyandrogen and testosterone concentrations.

Since only two stallions were captured in September, these data did not lend themselves to statistical analysis and are therefore not considered here. The 17-beta-hydroxyandrogen nadir occurred in December (2.11 ± 0.39 ng/ml). Disregarding the two stallions in September, the testosterone nadir also occurred in December (1.55 ± 0.34 ng/ml) and the peak in May (3.04 ± 0.36 ng/ml).

When seasonal testosterone concentrations were examined as a percentage of the total androgens, the results were as follows: September=58%, October=67%, December=73%, March=81%, May=85%, and July=80%. As total 17-beta - hydroxyandrogen concentrations increased, the proportion which constituted testosterone increased dramatically (Kirkpatrick et al., 1977).

Immature Stallion Androgens: The testosterone levels for the twenty-one two-year-old stallions are shown in Figure I. The 19 two-year-old males with undescended testes had a mean testosterone concentration of 1.14 ± 0.23 ng/ml of plasma. The two two-year-olds with descended testes had concentrations of 1.9 and 4.8 ng/ml with a mean of 3.35 ng/ml.

Discussion

It is clear that in the three wild stallions examined a definite diurnal variation exists with regard to plasma testosterone. Diurnal testosterone variations have also been demonstrated in man (Faiman and Winter, 1971; Barberia and Cortes-Gallegos, 1973; Leymarie et al., 1974); the rat (Kinson and Liu, 1973); and the rhesus monkey (Goodman et al., 1974). Increased testosterone levels have been shown to occur in rams (Wetteman and Desjardins, 1973) during the dark hours. While not as clearly evident as in other species, the data of Katongole et al. (1971), imply a diurnal testosterone variation in bulls. In domestic horses, several investigators have noted diurnal variations of plasma testosterone (Ganjam and Kenney, 1974; Cox and Williams, 1975; Sharma, 1976).

The pattern of changes of plasma testosterone in the wild stallions is qualitatively similar to those seen in rats and man, with the nadir occurring between 1900 and midnight and the highest concentrations occurring between 0600 and noon, and differs from that of the rhesus monkey where highest concentrations occur at 2100. In several breeds of domestic horses, Ganjam and Kenney (1975) noted a diurnal variation of plasma testosterone, ranging from 4.2 ± 0.4 ng/ml at 0600 to 3.0 ± 0.3 ng/ml at 1800. These values are quantitatively similar to those found in the wild stallions. Cox and Williams (1975) examined diurnal variations of plasma testosterone in Welsh Pony stallions during April and June and noted irregular patterns of secretion.

The 24-hr mean testosterone concentration for the bachelor stallion (B) was significantly lower ($P < 0.01$) from the mean testosterone concentrations in the two stud stallions. Both the stud stallions have been successful in recent years, in gathering and maintaining a harem and both are assumed to have sired colts. The bachelor stallion, however, has not demonstrated even an effort to gather a harem. This is highly unusual for an eight-year-old wild stallion (Hall, 1972). Whether the significantly lower testosterone concentration represents a cause or an effect of such sexual disinterest is unanswered by this study.

When the mean testosterone concentrations of the wild stallions are compared with those of rats (Bartke et al., 1973); man (Faiman and Winter, 1971); the rhesus monkey (Goodman et al., 1974); the ram (Wetteman and Desjardins, 1973); and the bull (Katongole et al., 1971) they appear to be quite low. The wild stallion study reported here was conducted in late October, during the non-breeding season. It has been shown that in both wild stallions (Kirkpatrick et al., 1977) and domestic stallions (Berndtson et al., 1974; Raeside, 1978) testosterone concentrations fluctuate seasonally and are relatively low in October.

The 34 wild stallions examined in the seasonal study showed androgen and testosterone concentrations below 2 ng/ml during the three non-breeding months and above 2.38 ng/ml during the breeding months. Peak breeding activity occurred at the same time as peak androgen/testosterone concentrations. Increased aggressiveness between males also coincided with the higher concentrations. Berndston, Pickett, and Nett (1974) reported seasonal changes in testosterone in Quarter Horse stallions. These variations were similar to those in the 34 wild horses, with the nadir occurring in October and the peak in May. Although it is not reported in their study, it is assumed that nutritional levels remained fairly constant throughout the year. If that is the case, then nutrition must not be the predominant stimulus for androgen/testosterone fluctuations in the Quarter Horse. Nutrition is very poor during the winter months for the wild horse and the annual 'green-up' occurred at the same time androgen levels began to increase. A more recent study (Thompson et al., 1977) failed to confirm this seasonal pattern of androgens in domestic stallions, yet Raeside (1978) demonstrated seasonal testosterone patterns in domestic stallions which were similar to those seen in feral stallions. Whether nutrition plays any significant role in regulating androgen levels remains unanswered at present, but from the comparison of events in the wild and domestic horse, it appears improbable. The marked seasonal change in androgen/testosterone ratio indicates that testosterone becomes the predominant androgenic steroid during the breeding season. Exactly what the large proportion of non-testosterone androgens consists of during the non-breeding season is unknown and remains to be examined. All samples were collected between 800 and 1600 hrs. The diurnal study indicates fluctuations are very small during this period of the day, and it is improbable that diurnal variations caused erroneous results in the seasonal data.

Although the sample size of two horses, in the immature stallion study, precludes definite conclusions, there appears to be a dramatic increase in plasma testosterone near the time young stallions are ejected from their bands. This increase in testosterone results in plasma concentrations similar to those in mature harem stallions. Since we have previously seen correlations between aggressive behavior and plasma testosterone concentrations, as well as seasonal behaviors associated with reproduction, it is reasonable to hypothesize that testosterone-induced behavioral changes, or testosterone-based pheromonal messages emanating from young stallions are ultimately responsible for their ejection from harem bands.

Acknowledgements

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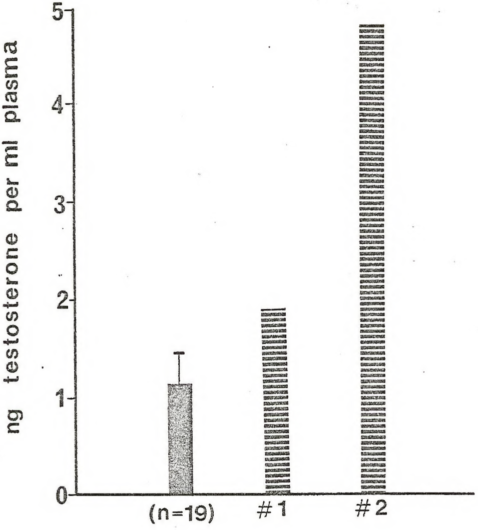

Fig. 1. Testosterone levels in 19 two-year-old males with undescended testes (solid bar) and two two-year-old males with descended testes (hatched bars).

Seasonal Estrus Patterns in Captive Feral Mares

Jay F. Kirkpatrick, John W. Turner, and R. M. Kenney
Department of Biological Sciences, Eastern Montana College, Billings

Abstract

Four feral mares from the Pryor Mountains were captured and held in captivity for 16 months. The mares, ages four, five, seven, and 15, were maintained on alfalfa hay, kept outdoors in an unprotected area and adjacent to a domestic stallion trained for teasing. Three mares were of proven fertility. Blood samples were taken by jugular venipuncture every three days and luteinizing hormone (LH) and total progestins (P) in plasma were measured. Cyclic estrus activity evidenced by mare behavior and plasma concentrations of LH and P began in early April and ceased prior to September. The seasonal estrus patterns correlate well with elimination behavior patterns associated with reproductive activities of feral horses in the Pryor Mountains, and with monthly foaling patterns of feral horses in both the Pryors (1974-78) and the Winnemucca District Range (1977). Length, frequency, and blood hormone values of the estrus cycle do not appear to be different from those in domestic mares, but the seasonal activity of feral mares stops sooner than in domestic mares living in similar latitudes. It is possible that this pattern represents selection against late foaling, which is associated with decreased chance of survival. Since the captive mares were kept on a relatively high plane of nutrition throughout the study, and since the onset of estrus activity in the spring was the same as in feral horses on the range, it is improbable that nutrition plays a significant role in initiating estrus cycle activity in sexually mature mares.

Testicular Biopsy in Feral Stallions

John W. Turner, Jr., R.M. Kenney, and J. F. Kirkpatrick
Department of Biological Sciences, Eastern Montana College, Billings

Abstract

Development of a simple testicular biopsy method for use in the field was investigated. Six feral stallions in the Pryor Mountains National Wild Horse Range in Montana were used in the study. Stallions were roped, taken to the ground, and mildly tranquilized. Due to the dangerous nature of the animal, all legs were restrained against the body by rope in a fashion which permitted access to the scrotum. After cleansing of the scrotum and sc injection of local anesthetic, a 1.0 cm incision was made to expose the tunica albuginea on the lateral (less vascular) surface of the testis. An area devoid of surface vascular supply was located, a 15-gauge biopsy needle was inserted through this site, and seminiferous tubules were collected from the middle or anterior portion of the testis. In two animals the needle was then reinserted through the same site and tubules were collected from the posterior portion of the testis. The samples were placed in fixative for histological analysis. After inspection for possible bleeding, the incision was closed with suture and sprayed with topical bacteriocide, and the animal was given tetanus toxoid and released. In one case slight (< 3 ml) bleeding occurred through the puncture site after biopsy. All animals immediately returned to normal activities after release, and subsequent observations indicated normal wound healing in all cases. Light microscopy revealed that each biopsy specimen contained cross sections of 10-18 seminiferous tubules. Active spermatogenesis evidenced by elongated spermatids in at least 20% of the tubules was present in all specimens except one. This sample was from a yearling with one descended testis and no spermatids were present in any tubules examined. No gross difference or difference in percent of active tubules was observed between samples from anterior and posterior regions of the same testis.

Introduction

In studying reproductive patterns and the regulation of fertility in feral stallions, it is valuable to examine parameters of hormone production and sperm production by the testes. Blood collection for hormone analysis is simple in stallions captured in the field. However, semen collection in the field is not feasible. Standard wedge section biopsy methods reported for the bull (Gassner and Hill, 1955; Knudsen, 1960) are too time-consuming for use in the field, and the possibility of infection and hematoma formation with its sequelae is significant. Although the use of needle biopsy in the testis has been reported for several domestic species, including the horse (McDonald, 1960; Galina, 1971), its potential in the field is unexplored. Therefore the development of a biopsy method which could be routinely used in the field was investigated.

Materials and Methods

Six feral stallions in the Pryor Mountain National Wild Horse Range in

Montana were used in the initial study. Five of these were mature stallions (> 3 years old) and one was a yearling with only one testis descended. The animals were captured at watering sites, led to a holding corral, roped and taken to the ground with a heading and heeling technique. Each animal was then tranquilized with a single intravenous injection of acepromazine (Ayerst, approximately 0.1 mg/kg body weight). To eliminate the danger of being kicked, all four legs were restrained against the body by rope in a fashion which permitted access to the genital region.

The scrotum was cleansed with surgical disinfectant and approximately 2 ml of 2% procaine hydrochloride (Cutter Laboratories) was injected subcutaneously into the scrotum and the injection site was massaged gently. The site chosen for injection and incision permitted access to the craniolateral surface of the testis, since Smith (1974) had reported that this was the least vascular area of the horse testis. After several minutes a 1.0 cm incision was made at the injection site to expose the tunica albuginea. An area devoid of surface vasculature was located, and a Tru-Cut disposable biopsy needle (Travenol) with a 20mm specimen notch was inserted into the testis through this site. The needle had been marked so that all specimens could be taken from the same depth, approximately 1 cm below the surface. The biopsy was obtained by retracting the outer cannula to expose the specimen notch, and then reclosing the cannula which cuts and secures the specimen in the notch. The needle was withdrawn and the specimen was placed in a 5% glutaraldehyde/phosphate buffer (pH 7.4) or Bouin's medium for fixation.

In four cases a single sample was taken from the anterior or middle region of the testis. Since it was possible that a single needle biopsy might not be representative of the whole testis, in two of the stallions two biopsies were taken from the same testis. One sample was taken from the anterior portion of the testis, and then the needle was reinserted through the same site and a sample was taken from the posterior portion of the testis. After inspection of the biopsy site for possible bleeding, the skin and muscle were closed with two sutures (00 Vicryl absorbable suture, Ethicon). The wound was sprayed with topical bacteriocide, and the animal was given tetanus toxoid (Cutter Laboratories) intramuscularly and released in the corral. After several days of observation the animals were returned to the range.

Tissue samples, each approximately 1 x 3 mm, were imbedded in paraffin or Spurr medium (Polysciences), stained with hematoxylin and eosin, sectioned at 1-5 microns thickness, and mounted on slides. Since needle biopsy provides a limited amount of tissue, an important question is whether the needle biopsy provides information which is representative of the whole testis. To investigate this, dual needle biopsies and testis wedge cross sections were compared in testes from eight domestic stallions. Five were normal and mature, one was unilaterally cryptorchid, and two were immature. From both the anterior and posterior region of each right and each left testis a 1 x 3 mm needle biopsy and a 1 cm^2 wedge were taken. The samples were fixed in Bouin's medium, imbedded in paraffin, sectioned at 5 μ, stained with hematoxylin and eosin, and mounted. The only morphological difference between needle biopsy and comparable wedge section was a greater percentage of distorted tubules in the biopsy tissue. This was not serious enough to prevent analysis. In the horse,as in a number of other species, a given tubular cross section contains cellular associations which are all at the same stage of spermatogenic development. The presence of maturing (elongated) spermatids at or near the tubular lumen represents an advanced stage of spermatogenesis (Swierstra et al., 1974). To determine whether spermatogenesis was occurring in samples in the present study, the percentage of tubules containing maturing spermatids at or near the lumen was determined. Counts were derived from the total number of tubules in each biopsy and from 100 tubules in each wedge section. To prevent bias, the observer was unaware of which biopsies and wedge sections were related.

Results

In three of six feral animals some bleeding occurred from superficial scrotal vessels during the biopsy procedure. In one case, slight (<3 ml) bleeding occurred through the puncture site after biopsy. All animals immediately returned to normal activities after release, and subsequent observation indicated normal wound healing in all cases.

In biopsies from mature feral horses, the percent of tubules containing maturing spermatids at or near the tubular lumen was 34.6 ± 9 sd. One animal was a yearling with one undescended testis, and no spermatids were present in any of the tubules examined. No gross difference or difference in percent of active tubules was observed between samples from anterior and posterior regions of the same testis. Cross sections from a biopsy of a feral stallion testis are presented in Plate 1.

In all biopsies from domestic horses an average of 30.1 ± 8 percent of the tubules contained maturing spermatids. Although percentage of tubules containing maturing spermatids varied among horses, the percentage in biopsies was not significantly different (t-test, $p > .05$) from that in associated wedge sections in any given horse (Fig. 1). No maturing spermatids were present in any biopsy or wedge section from immature horses. To compare left and right testes, data from wedge section and biopsy were pooled. With the exception of the unilaterally cryptorchid stallions, the percent of tubules with maturing spermatids in the left testis was not different (t-test, $p > .05$) from that in the right testis in any horse (Fig. 2). Furthermore, based on pooled data from wedge section and needle biopsy on left and right side, no significant difference (t-test, $p > .01$) between samples from anterior and posterior regions was observed in any testis (Fig. 3).

Discussion

Hemorrhage associated with biopsy and the possible deleterious effects of its sequelae on sperm production have been reported (Knudsen, 1960). In the present study only one of six biopsies resulted in intratesticular bleeding. The effects, if any, on sperm production in that testis are unknown, since there was no follow-up study. It is unlikely that the animal's fertility was impaired, since the other testis was not involved. Since the data obtained from domestic horse testes indicated no difference between left and right testis samples, only unilateral biopsy should be necessary, and risk of infertility due to biopsy would be minimized.

Based on the small sample size studied in domestic horse testes, it appears that dual needle biopsy does provide a reasonably representative sample of testicular tissue. Both wedge section and biopsy indicated reasonable uniformity between left and right testis and between anterior and posterior regions of the same testis. The average percentage of tubules containing maturing spermatids in feral horses was similar to that in normal domestic horses. Although direct comparison is not possible, these percentages appear to be in reasonable agreement to those reported by Swierstra et al. (1974) for comparable stages in their stallions.

The major disadvantage of the biopsy is the small number of tubules available in a sample. It is not feasible to quantitatively evaluate spermatogenesis when samples may have as few as 25-30 tubules. However, a needle biopsy can permit differentiation of normal sperm production from azoospermia or severe oligospermia as evidenced by biopsies from the unilaterally cryptorchid stallion in the present study. In studies of effectiveness of antispermatogenic agents, for example, where severe depression in sperm production may be expected, the needle biopsy can be a useful tool.

In summary, the results of this study show that (1) the needle biopsy method provides a reasonable means of collecting testicular material from feral stallions in the field and (2) such biopsies appear to be generally representative of spermatogenic activity in the testes.

Acknowledgements

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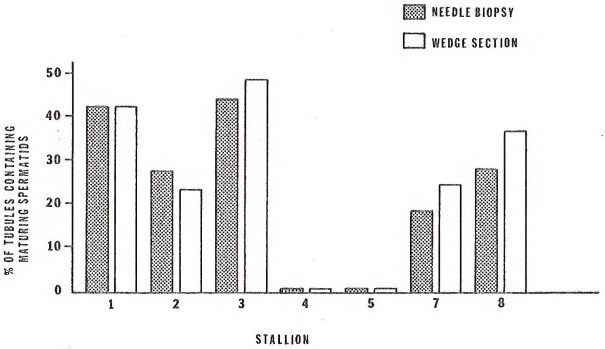

Figure 1. Comparison of spermatogenic activity determined by wedge section and needle biopsy. Stallions 1, 2, 3, 7, and 8 are mature and normal; stallions 4 and 5 were immature.

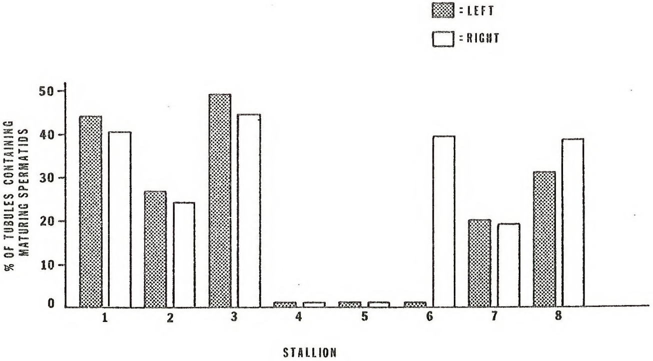

Figure 2. Comparison of spermatogenic activity in left and right testes. Data from wedge section and needle biopsy were pooled. Stallions 1, 2, 3, 7, and 8 are mature and normal; stallions 4 and 5 were immature; stallion 6 was unilaterally (left side) cryptorchid.

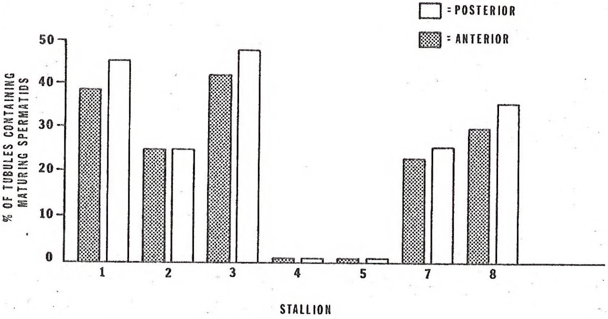

Figure 3. Comparison of spermatogenic activity in anterior and posterior regions of the testis. Data from wedge section and needle biopsy on left and right side were pooled. Stallions 1, 2, 3, 7, and 8 were mature and normal; stallions 4 and 5 were immature.

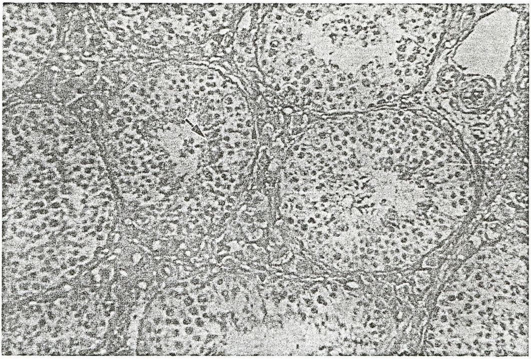

Plate 1. (A) 60x

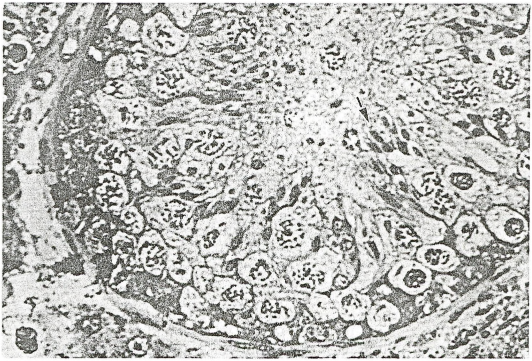

Plate 1. (B) 200x

Cross section of biopsy from normal feral stallion testis. Arrows indicate maturing spermatids.

Adrenal Corticosteroids and Their Use in Monitoring Stress in Captive Feral Horses

Jay F. Kirkpatrick, J. W. Turner, Jr., R. M. Kenney, and V. K. Ganjam
Department of Biological Sciences, Eastern Montana College, Billings

Abstract

In the course of studies involving captive feral horses, capture techniques and handling procedures are such that some degree of stress is usually induced. Baseline values for total corticosteroids as well as diurnal variations were determined in captive stallions. Three unstressed stallions had a 24-hr. average total corticosteroid concentration of 40.2 ± 6.3 (S.D.) ng/ml of plasma, with a nadir occurring at 11:00 pm (27 ± 7.4 ng/ml) and a higher plateau between midnight and 5:00 am with values from 37 to 51 ng/ml. The cortisol:corticosterone ratio was 168:1. Both the cortisol:corticosterone ratio and the diurnal pattern differ from the same parameters in domestic horses. One hundred-thirty-seven feral horses from Montana were captured and handled, restrained, and bled by one of three methods. These included: (1) jugular venipuncture from standing restrained horses, (2) jugular venipuncture from horses brought down by roping, i.e., heading and heeling, and (3) indwelling catheter in standing restrained horses. Plasma corticosteroids were quantitated and the values were used to evaluate the three procedures with regard to stress. The results indicated no significant differences ($P < .05$) among the mean corticosteroid values for the three handling procedures. Two horses out of 137 showed significantly elevated corticosteroid levels ($P < .05$) and were easily and visibly identifiable as severely stressed. Measurement of plasma corticosteroid levels appears to be a useful, accurate, and relatively inexpensive means to evaluate handling procedures for feral horses.

Age Characteristics of Feral Horses in Montana

Anne Perkins
Department of Biological Sciences, Eastern Montana College, Billings

Els Gevers
Department of Animal Husbandry, Landbouw Hogeschool, Wageninge, Netherlands

John W. Turner, Jr.
Department of Physiology, Medical College of Ohio, Toledo

Jay F. Kirkpatrick
Department of Biological Sciences, Eastern Montana College, Billings

Abstract

The population dynamics and age characteristics of feral horses in Montana were studied over a four-year period (1974-1978). The herd size ranged from 95 to 168 horses. Fifty-two horses were removed through Adopt-A-Horse and approximately 71 died from natural causes. The age profile of the herd indicates that almost 50% of the horses were three years old or less, and the female:male ratio was two:one. Over the four years the average age of the horses ranged between 6.26 and 6.7 years and did not differ significantly. Dominant harem stallions averaged 12.8 years, and non-dominant harem stallions averaged 1.7 years of age. Bachelor stallions averaged 6.1 years of age and lead mares averaged 12.2 years. One hundred and three foals were born and survival through their first year ranged from 38% to 100%. The reproductive age of mares ranged from three to 21 years. Nineteen of 21 two-year-old males examined had undescended testes and were permitted to remain with their respective harems. Two two-year-old males had partially descended testes but no signs of spermatogenesis. Both of these horses had been ejected from their harems. Normally, young stallions are permitted to remain with their harems until age three. A sex ratio of 2:1 female:male appears to stabilize social structure of the herd.

Introduction

Although there are presently an estimated 70,000 feral horses inhabiting public lands in ten western states, very little is known about the population dynamics and age distributions of these horses. The studies of Feist (1971), Pellegrini (1971), and Hall (1972) were the first systematic attempts to gather data on population characteristics and social structure of America's feral Equidae. While the results of these three studies provided a foundation for our early understanding of feral horses in North America, there were limiting factors imposed upon the investigations. Two of the three studies were of a short-term nature (one year or less) and only Hall's work provided any aging data.

For a variety of reasons, the precise age profiles for the various herds are not well understood, usually because fiscal restraints prohibit the acquisition of age data from large numbers of animals. In the Pryor Mountains of south-central Montana, on the 45,000 acre National Wild Horse Range, a herd of feral horses has been studied over a four-year period, from 1974 to 1978. The purpose os this study was to provide a more accurate picture of age profiles as they relate to herd social structure and reproduction. Since the feral horse herds of the western United States do not represent a homogeneous group of animals, it should be noted that these data and the accompanying conclusions are applicable only to the Pryor Mountain horses.

Methods and Materials

During the four years encompassed in this study (September, 1974 through July, 1978), 73 feral horses were captured and aged. Another 124 horses were aged prior to 1974. Most often, the horses were driven or lured with water into holding pens and corrals. Once in the corrals, each animal was roped by the head and hind legs and gently stretched out until it went down ("heading and heeling"). Animals were lip tattooed, and aging was accomplished by evaluating tooth replacement and wear. In addition, each animal was identified by unique markings and harem band affiliation. The animals were released after they were aged. It is important to note here that age data derived from tooth replacement and wear must be carefully evaluated. Accurate aging of horses by this method is not difficult through eight years of age. Beyond that age range, the difficulty increases (Ensminger, 1951). One technical problem involves horses living on gritty, sandy soils where tooth wear will occur very fast (Bone, 1964). The Pryor Mountains possess such a soil type. In this study, however, over 85% of the horses were aged before they reached eight years, providing accurate data. Over 650 hours of direct observation of the horses were carried out between September, 1975 and July, 1978. In almost all cases, observation was accomplished with the aid of spotting scopes without disturbing the observed animals. As animals were observed, unique markings permitted the gathering of age data. Where possible, data are presented as means ± standard deviation. Student's t-test was used to evaluate differences for statistical significance.

Results

Over the four-year period the herd size ranged between 95 and 168 animals. Ninety-five percent of this population was aged as described. Table I indicates the total population profile for the study period. Table II indicates the age class and sex of horses removed through the Adopt-A-Horse program during this study. Figure I indicates the age distribution of the herd in August, 1977. At this time, the horse herd was at maximum size and had suffered few losses, either through Adopt-A-Horse or through natural causes for two years.

The horses were found in harem groups, each consisting of a mature stallion (three years or older) and a number of mares, all-stallion bachelor groups, or in the case of very old stallions, alone. These social groups have previously been described by Hall (1972) and Feist (1971). The number of harem groups ranged between 19 and 27 over the four-year period. All changes in the number of harem groups from year to year were caused by the removal of excess horses as part of the Adopt-A-Horse program or by natural attrition during the winter and spring months. Harem groups ranged in size from two to ten animals with a mean of 4.9 ± 2.0. The mean number of stallions per harem was 1.7 and in only two cases did a harem have more than one mature stallion. In both these cases, the harem consisted of ten horses. Also, in both cases, one of the two stallions remained behaviorally subordinate to the other. In both cases, it was the older stallion which was dominant. No observations were made of subordinate stallions attempting to mate harem mares. The ages of all harem stallions ranged from eight to twenty years with a mean of 12.8 ± 4.0. The ages of immature harem males ranged from new foals to three years with a mean of 1.7 ± 0.4.

The day-to-day activity of the harem is normally directed by a lead mare. Twenty-one lead mares were identified during the study and the mean age of this group was 12.1 ± 3.1 years. The sex ratio of the herd was almost exactly 2:1 female:male, however, this was primarily the result of removal of larger numbers of males from the range prior to 1974.

Six different bachelor groups were identified during the course of this study and all were composed of either two or three stallions. Their ages ranged from three to eight years with a mean of 6.1 ± 1.3 years. A total of six lone stallions were observed during the study. Of these, four were of known age. The mean was 16.1 ± 3.1 years.

During five consecutive foaling seasons, 103 live foals were born. At birth, the sex ratio was 2:1.88 female:male. Foal survival through their first year ranged from a high of 100% in 1976/77 to a low of 38% in 1974/75. The mean foal survival to age one for the four years was 75%. The ages of reproductive mares ranged from three to twenty-one years, with a mean of 8.4 ± 3.9 years.

Twenty-one two-year-old males were examined. All but two possessed undescended testes and were permitted by their respective harem stallions to remain in their harems. The two two-year-olds with partially descended testes were both driven from their respective harems during their second spring.

Discussion

The number and size of the harem groups remained remarkably stable over a four-year period and were quite similar to the data of Hall (1972) and Feist (1971) from the Pryor Mountains and of Pellegrini (1971) in Nevada. The mean age of horses in the Pryor Mountains also remained stable and did not differ significantly ($p < .05$) over the four-year period. During the study period, there were two years when foal survival was 100% (a total of 38 foals reached one year successfully), and 26 one-year-olds were excessed through Adopt-A-Horse. These factors served to offset one another and to stabilize the average age.

The mean age of harem stallions was reported by Hall (1972) to be 7.8 years. Our data indicated the mean age of harem stallions to be 12.8 ± 4.0 years. This is also considerably older than the mean age of all males in the herd (7.2 ± 6.1 years). This upward trend in the age of harem stallions is possibly the result of fewer males in the herd and less competition for the mares.

The lead mare of the harem has been described previously by both Feist (1971) and Hall (1972). The mean age of lead mares (12.1 ± 3.1 years) was significantly older ($p < .05$) than the mean age of all mares (6.3 ± 3.1). This difference, once again, suggests a behavioral dominance imparted by increased age.

There are very little data available regarding bachelor stallion groups. Both Hall (1972) and Feist (1971) reported the existence of these groups, but neither study addressed the subject of age. The average age of 6.1 ± 1.3 for bachelor stallions must be viewed with caution, since a large number of horses removed in Adopt-A-Horse program are juvenile males. Under more natural conditions, it might be expected that bachelor stallions would be, on the average, younger than 6.1 years.

The reproductive lifespan of feral mares appears to be greater than Hall (1972) estimated. Hall reported a reproductive lifespan of five or six years, beginning at four years and ending at about nine years. In contrast, we found a range from three years to twenty-one years, with a mean age of 8.4 ± 3.9 years. Tyler (1972) reported that New Forest pony mares did not foal until age three or four (the same as in feral mares); however, there were no data from that study regarding reproductive lifespan.

Previous studies provide very little data regarding survival rates of foals through their first year. The lack of sound data on this subject has been the focal point in several legal cases involving feral horse management in the United States. Our data indicate a range of 38% to 100% survival over four years and make it clear that generalizations about survival should be made with caution. According to the B.L.M., range conditions in the Pryor Mountains have been improving during the course of this study. The herd size has remained relatively stable. The major variable was weather conditions during the winter and spring. The winters/springs of 1975/76 and 1976/77 were extremely mild, and those of 1974/75 and 1977/78 were extremely harsh.

As reported earlier by Feist (1971) and Hall (1972), there are few instances of reproductively active males, other than the harem stallion, remaining in the harem group. We found the mean age of subordinate harem males to be 1.7 ± 0.4 years, i.e., sexually immature.

Both Hall (1972) and Feist (1971) noted that feral stallions reach sexual maturity later than their domestic relatives (three years vs. eighteen months). The cause(s) of this delay is unknown but may involve nutrition and/or genetics. It is clear, however, that sexual maturity and descent of the testes occur at the same time and trigger, in some way, the expulsion of young stallions from the harem.

Acknowledgements

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TABLE 1

TOTAL POPULATION PROFILE

AUGUST 1974 - JULY 1978

	1974[1]	1975	1976	1977	1978[2]
LIVE FOALS BORN	24	13	25	24	17
ANIMALS REMOVED[3]	0	27	0	25	0
MORTALITY	15	15	0	0	41
BASE POPULATION[4]	148	119	143	142	118
AVERAGE AGE (± S.D.)	6.5 ± 7.9	6.26 ± 4.2	6.7 ± 4.5	6.6 ± 4.9	6.9 ± 5.1

[1] AUG. - DEC.

[2] JAN. - JULY

[3] ADOPT-A-HORSE PROGRAM

[4] DECEMBER OF EACH YEAR

TABLE 2

AGE AND SEX OF EXCESSED HORSES

Age Class (Yrs.)	1975		1977	
	Male	Female	Male	Female
1	4	6	4	12
2	1	2	4	2
3	1	2	1	1
4	1	0		
5	2	0		
6	1	0		
7	1	1		
8	3	1		
10	1	0		
19			1	
	15	12	10	15

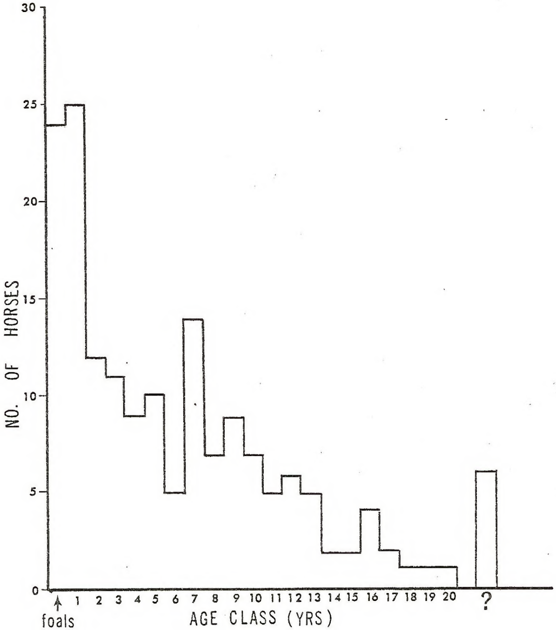

Fig. 1. Age distribution of the Pryor Mountain Feral Horse Herd in August, 1977.

Sociosexual Behavior in the Domestic Pony

Cheryl S. Asa
Department of Veterinary Science, University of Wisconsin, Madison

Introduction

Although many behavioral questions may be best answered by studies of animals in their natural habitats, physiological investigations often require the use of captive or domestic species. Our work on the reproductive behavior and physiology of the mare has focused, for practical reasons, on the domestic pony. Harem groups have been used for behavioral testing to approximate natural social conditions and to allow analysis of the interaction of physiological and social parameters.

This paper summarizes a series of studies on the sexual behavior and physiology of the pony (160-250 kg), including ovariectomized mares as well as intact mares during the ovulatory and anovulatory seasons. A justification for extrapolating this work on domestic ponies to feral horses is that domestic ponies have probably been subject to less intense selective breeding than horses. Also, the breeding season of the pony is shorter and better defined than that of the horse, and thus probably more similar to the feral animals. Wisconsin ponies, maintained outdoors in small herds year round, have ovulatory cycles from April to October (Ginther, 1974) whereas some horses (20%) do not enter an anovulatory period (Ginther, 1979). Feral mares from the Pryor Mountain range have a breeding season that extends from April until August (Kirkpatrick, personal communication).

Experiment I: Sociosexual Behavior of the Mare

A basic study of the social and sexual behavior of ponies maintained in harem groups was undertaken to investigate the relationships between physiological events (e.g. follicular growth and ovulation) and the behavioral changes of the periovulatory mare, including the social dynamics of the entire group. A more detailed report of this experiment can be found in Asa, Goldfoot, and Ginther (1979).

The six mares were of mid-reproductive age (8-12 years) and the two stallions approximately 10 and 20 years. Prior reproductive histories of the animals were unknown. Two harem groups, each consisting of one vasectomized stallion with the same three mares, were assembled daily for behavioral testing. Group composition was constant throughout the experiment. Between tests, the mares were pastured together, while the stallions were stabled separately.

The study extended from July 25 to September 6, 1977. Daily tests were conducted between 11 AM and 2 PM, one hour per group, in an outdoor paddock approximately 6 by 9.6 m. The categories of behaviors monitored included vocalization, proximity, olfactory and tactile investigation, proceptivity, marking, aggression, and copulation. Definitions of the social and sexual behaviors analysed can be found elsewhere (Asa, Goldfoot, and Ginther, 1979). Following the behavior tests, mares were palpated rectally to monitor follicular growth and ovulation. Diestrous mares were palpated every third day and estrous mares daily.

Fifteen behavioral estrous periods occurred during the course of the study. The estrous phase of the cycle consisted of an average of 5.5 days before and two days after ovulation. Behavioral changes accompanying estrus in the mare included increased frequencies of approaching and following the stallion, urinating, clitoral winking, presenting and tail raising. Changes in spatial orientation consisted of standing apart from other mares or near to the stallion with tail raised.

Comparison of the mean frequencies of selected behaviors observed during estrous, diestrous, and transitional phases are presented in Figure 1. Estrus was behaviorally defined as the display of more than one urination and more than one min of tail raise near stallion (TRNS) per one-hour test. The transitional phase was comprised of one day on either side of estrus, and diestrus was all other days.

Experiment II: Sexual Behavior of Ovariectomized and Seasonally Anovulatory Mares

Typically, female mammals exhibit sexual behavior only during fertile phases of their breeding season or estrous cycle. As summarized in Figure 2, hormonal stimulation provided by the developing follicle(s) consists of estrogens and possibly androgens, although many rodents and domestic ungulates require the presence of progesterone for full expression of estrous behavior (Clemens and Christensen, 1975). When the ovaries of any of these females are removed, sexual behavior is typically eliminated (Young, 1961).

Exceptions to this general pattern have been found among the primates, most importantly the human, but also the rhesus and stumptail macaque. In these species, sexual receptivity may occur regardless of the phases of the ovarian cycle although sexual activity may be more likely during the periovulatory period (Baum, Everitt, Herbert, and Keverne, 1977). Following ovariectomy, levels of sexual behavior may be reduced in some individuals, but usually continue (rhesus: Baum et al., 1977; stumptail: Slob, Wiegand, Goy, and Robinson, 1978).

Because signs of estrus had been observed in seasonally anovulatory (Van Niekerk, 1967; Ginther, 1974; Webel, Harland, and Dzuik, 1977) and ovariectomized mares (Garcia, published in Ginther, 1979), a detailed investigation of the behavior of mares in these two conditions was initiated. A more complete account of this study appears in Asa, Garcia, Goldfoot, and Ginther (in press).

Ten ovariectomized (OVEX) and ten seasonally anovulatory (ANOV) mares were used. Sexual experience of the mares before ovariectomy was not known. The ANOV mares were selected after rectal palpation revealed involuted ovaries with follicles no more than 10 mm diameter. The animals were maintained as in Experiment I.

Behavior tests were conducted daily from January 9 to 23, 1978, in the early afternoon, 20 min per group. Five harem groups, each consisting of two OVEX and two ANOV mares plus one stallion, were assembled randomly each day. Behaviors scored were the same as those of Experiment I.

The intensity of estrus seen in OVEX and ANOV mares was most similar to that seen in periovulatory mares on the first, second, and last days of the seven-day estrous phase. Gross inspection of the reproductive tract and histological examination of the ovarian pedicles of one of the ovariectomized mares revealed no traces of ovarian tissue.

All the OVEX and ANOV mares displayed estrous signs on at least one of the test days, although estrous intensity was sometimes low. Male approaches, precopulatory investigation and stimulation similar to that shown to the periovulatory estrous mares in Experiment I, as well as the complete male ejaculatory pattern, demonstrated that both the OVEX and ANOV mares were attractive and receptive to the stallions.

No statistical differences were found between the two groups of mares on any of the behavioral endpoints analyzed. The ANOV group had one mare that was in weak estrus on only one day, but another that showed full estrus for 14 days. The OVEX group also had one mare that was only in weak estrus for one day, but another that displayed full estrus for all 15 days. The overall pattern of estrous expression across days was irregular (Fig. 3).

Experiment III: The Effects of Dexamethasone Suppression of the Adrenal Cortex on Sexual Behavior of the Ovariectomized Mare

In Experiment II, the ovariectomized mares were not subject to hormones of ovarian origin and the seasonally anovulatory mares were probably affected only minimally. Because no evidence exists for non-hormonal mediation of sexual behavior in non-primates, an extra-ovarian source of steroid, such as the adrenal cortex, seemed likely. As demonstrated for the female rhesus macaque, sex steroids secreted by the adrenal cortex can induce estrous behavior (Everitt and Herbert, 1971; Everitt, Herbert, and Hamer, 1972; Johnson and Phoenix, 1976). Therefore, dexamethasone, a synthetic corticosteroid which suppresses the synthesis of steroids in ACTH, sensitive tissues (i. e., the adrenal cortex), was chosen for an investigation of the ability of the adrenal to affect the sexual behavior of the mare. Due to a concern that dexamethasone might prevent estrous behavior by some means other than suppression of the adrenal (e. g., debilitating side-effect or the binding of E_2 receptors), a treatment group given dexamethasone plus estradiol was included. This experiment constitutes one part of a study reported in Asa, Goldfoot, Garcia, and Ginther (in press).

Twelve mares and four stallions were given 20 min behavior tests daily from May 7 to 11, 1979, to provide data for matching mares on measures of estrus before assignment to treatment groups. Matched-threes were then randomly assigned, one to each of three treatment groups: dexamethasone (DEX), dexamethasone plus estradiol (DEX + E_2), or control. DEX (30 mg) or DEX + E_2 (30 mg and 1 mg respectively), were administered IM from May 15 to 26, 1979. The DEX was given in a divided dose twice daily at 7AM and 6PM and the E_2, dissolved in corn oil, once daily at 7AM. Penicillin/streptomycin was injected once daily at 6PM as a prophylactic. Control mares were given sham injections.

Four harem groups, each composed of three mares (1 DEX, 1 DEX + E_2, and 1 control) plus one stallion, were assembled randomly each day between 1 and 3PM for the 20 min behavior tests. Behaviors recorded were as in Experiment I.

The incidence of estrous and copulatory behavior was significantly reduced in mares treated only with dexamethasone. These mares had lower mean scores than the DEX + E_2 and control mares on all measures of estrus, mean frequencies of stallion precopulatory investigation (sniff, lick, nibble, nuzzle), and copulatory behavior (Fig. 5). No significant difference was found between the control and DEX + E2 mares for number of days of weak or full estrus, frequency of female approach and follow, urination, or mount, for mean duration of tail raise near stallion (Fig. 4). Male approach was not different among the groups. The control group received more intromissions and ejaculations than either the DEX or DEX + E_2 groups.

General Discussion

The results of these experiments reveal that ovariectomized and seasonally anovulatory mares display estrous behavior similar to that of periovulatory mares and that this behavior is likely influenced by steroids secreted by the adrenal cortex. Additionally, these findings suggest that sexual behavior may serve functions beyond reproduction in this species. Anovulatory females from no other species have been reported to engage in copulation to ejaculation, although in primates, where exceptions might be expected, no data are available.

The data for the ovariectomized mare are similar to those for some primate species. There appear to be no reports that the libido of the human female is affected by ovariectomy. Ovariectomy reduces, but does not eliminate, the sexual receptivity of the rhesus and stumptail macaque. Subsequent adrenalectomy, however, reportedly diminishes receptivity for the human (Waxenberg, Drellich, and Sutherland, 1959) and the rhesus female (Everitt, Herbert, and Hamer, 1972). The ovariectomized, estrogen-maintained rhesus also shows a suppression of sexual behavior following dexamethasone administration (Everitt and Herbert, 1971). Sexual performance of the stumptail macaque female has not been affected by either ovariectomy (Slob, Wiegand, Goy, and Robinson, 1978), dexamethasone treatment (Goldfoot, Wiegand, and Scheffler, 1978; Baum, Slob, de Jong, and Westbroek, 1978), or adrenalectomy (Baum et al., 1978).

The pattern that emerges for the mare (Fig. 7) appears to be a combination of the typical mammalian pattern (Fig. 2) and that seen in some primates (Fig. 6). The exception to the mammalian pattern shown by the human female was interpreted as evidence for the supposed emancipation of the human from the biological or physiological constraints imposed on "lower" species. Further justification was based upon the highly evolved social system of the human. The recent evidence that the sexual activity of other primates may not be controlled exclusively by ovarian hormones, and for the stumptail, perhaps not by hormones at all, may be accounted for by the not so divergent phylogeny of the human and the non-human primates. The addition of *Equus caballus* to the small number of species that engage in social or non-reproductive sex cannot be explained by phylogenetic proximity. Rather, due to environmental pressures, the cohesiveness of the social groups formed by these primates and by *E. caballus* may have become important for survival.

The factors which influence whether the primary social unit seen in feral horses in a particular area is uni-male (harem) or multi-male have not yet been determined. All feral horse bands studied to date, however, display strong social bonds, with the male-female reproductive units remaining together throughout the year instead of assembling only for the breeding season. This type of stable social unit apparently has not been reported for any other nondomestic ungulate except for some species of zebra, also of the genus *Equus*.

Welsh (1975), in his study of the Sable Island ponies, suggested that the stallion may be necessary to the winter survival of mares and young. Sable Island bands which lost their stallions and were subsequently taken over by an unproved stallion suffered higher than average mortality. There was no information on bands without stallions, presumably because they were not observed.

The factors that influence a stallion to remain with his band, once reproductive activity has ceased, or to acquire a band during the non-breeding season, may include social, or non-reproductive sex. The ovariectomized mare represents an experimental manipulation which does not occur in the natural state. Non-pregnant mares, however, do become anovulatory at the end of the breeding season. Pregnancy rates for domestic mares are about 80%, with 70% carried to term (Ginther, 1979). In free-ranging herds, it is estimated that 40-50% of the mares fail to deliver live young each spring (Nelson, in press; Feist and McCullough, 1975). Thus, estrus may be displayed by some percentage of feral mares during the winter months. Unpublished observations of estrous behavior in three prepuberally ovariectomized yearling mares, by Wesson from this laboratory, indicate that ovarian activity is not necessary for the initiation of sexual behavior. Therefore, even young females which had not ovulated or experienced copulation during the breeding season might still exhibit sexual solicitation during the anovulatory season. Sexual activity by non-pregnant mares at times when conception is impossible may have functional significance by contributing to the maintenance or formation of social bonds.

Acknowledgements

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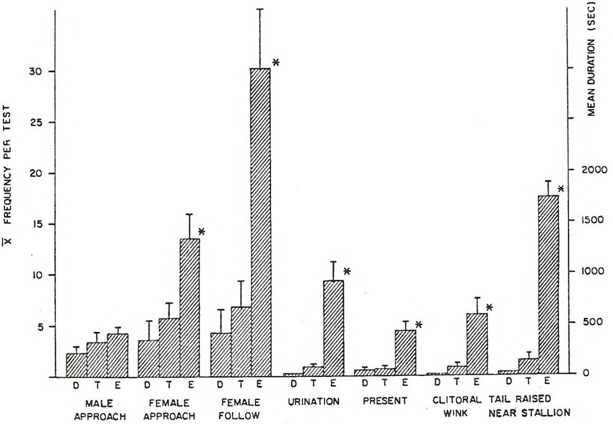

Figure 1. Comparison of changes in mean duration (for tail raise near stallion) and frequency (all others) of selected behaviors during diestrous (D), estrous (E), and transitional (T) phases (transition defined as one day on either side of the estrous phase). E was greater than D and T for all behaviors but male approach.

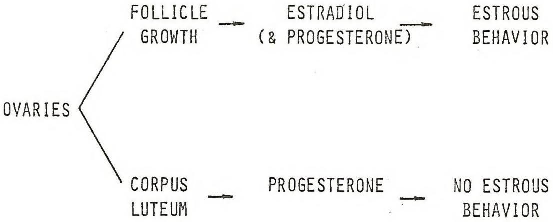
FOLLICLE GROWTH
ESTRADIOL (& PROGESTERONE)
ESTROUS BEHAVIOR
OVARIES
CORPUS LUTEUM
PROGESTERONE
NO ESTROUS BEHAVIOR

Figure 2. Typical mammalian pattern of ovarian structures, their secretory products, and influence on sexual behavior.

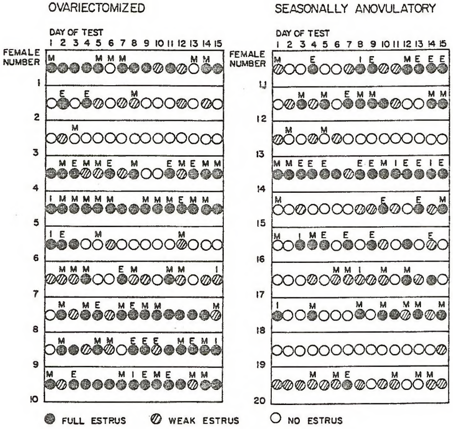

Figure 3. Pattern of incidence of full, weak, or no estrus for ten OVEX and ten ANOV mares during 15 consecutive days of testing in harem groups. E, ejaculation; I, intromission; M, mount.

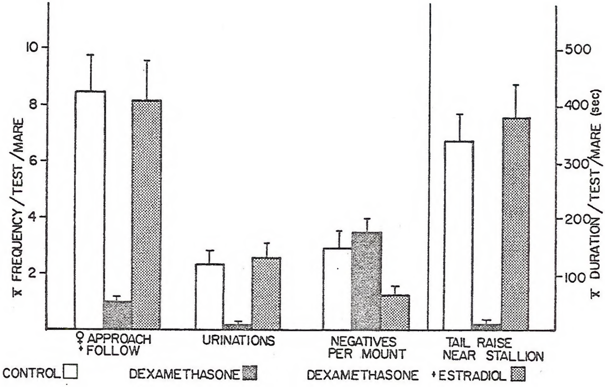

Figure 4. Mean frequency or duration per test of selected proceptive behaviors of control, dexamethasone, and dexamethasone plus estradiol-treated mares.

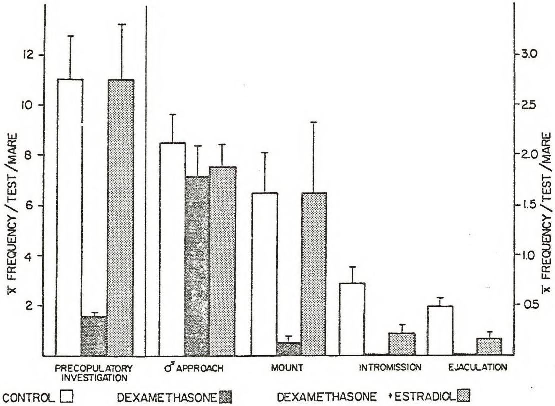

Figure 5. Mean frequency per test of selected stallion behaviors involving control, dexamethasone, and dexamethasone plus estradiol-treated mares.

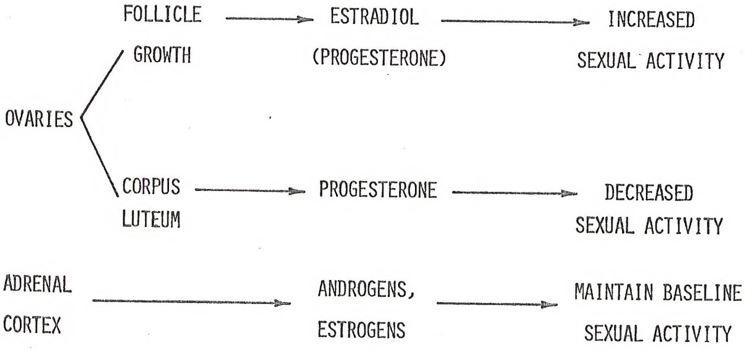
FOLLICLE
GROWTH
ESTRADIOL
(PROGESTERONE)
INCREASED
SEXUAL ACTIVITY
OVARIES
CORPUS
LUTEUM
PROGESTERONE
DECREASED
SEXUAL ACTIVITY
ADRENAL
CORTEX
ANDROGENS,
ESTROGENS
MAINTAIN BASELINE
SEXUAL ACTIVITY

Figure 6. Ovarian and adrenal influence on sexual activity of the female rhesus monkey.

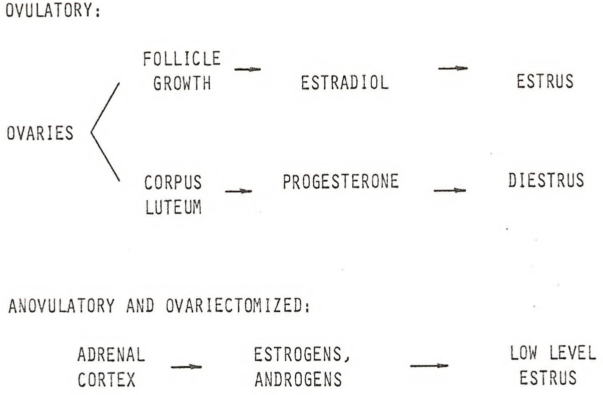
OVULATORY:
FOLLICLE GROWTH
ESTRADIOL
ESTRUS
OVARIES
CORPUS LUTEUM
PROGESTERONE
DIESTRUS
ANOVULATORY AND OVARIECTOMIZED:
ADRENAL CORTEX
ESTROGENS, ANDROGENS
LOW LEVEL ESTRUS

Figure 7. Postulated influence of the ovary on estrous behavior during the ovulatory season and of the adrenal during the anovulatory season or following ovariectomy in the mare.

The Feral Asses (*Equus asinus*) of Ossabaw Island, Georgia: Mating System and the Effects of Vasectomies as a Population Control Procedure[1]

William D. McCort
The Pennsylvania State University, University Park

Abstract

The objective of this study was to analyze the social organization, and in particular the mating system of the feral asses on Ossabaw Island, Georgia. The 80 feral asses assorted themselves into eight to 11 relatively stable groups which varied from four to 22 individuals. There were three distinct types of groups: I. Groups with one adult male and one to several adult females with offspring; II. Groups with one dominant adult male, one to several subordinate males, and several adult females with offspring; III. Bachelor groups composed of adult males. The reproductive strategy of each male varied with the type of group he was in. In all three group types, male reproductive success (RS) was much more variable than female RS. Vasectomies performed as a population control procedure did not alter the overall social organization of the feral asses. However, the vasectomies did result in female asses maintaining abnormally long attachments to their last born young, and eventually the unusual mating of the young males within their family groups.

Introduction

Equid social organizations have generally been described as either harem groups with one adult male and females with offspring, or highly unstable groups with no lasting association between individuals besides mother-offspring relationships. Those equids having the harem group social organization include Plains zebras (*Equus quagga*, Klingel, 1969b, 1972); Hartmann's zebras (*E. zebra hartmannae*, Joubert, 1972; Klingel, 1968); Cape mountain zebras (*E. z. zebra*, Klingel, 1968, 1969a, 1972); and feral horses (*E. caballus*, Berger, 1977; Feist, 1971; Feist and McCullough, 1975, 1976; Tyler, 1972). Equids with unstable groups include Grevy's zebra (*E. grevyi*, Klingel, 1969c, 1972), African wild asses (*E. africanus*, Klingel, 1972, 1977), Asiatic wild asses (*E. hemionus*, Klingel, 1977), and feral asses (*E. asinus*, Moehlman, 1974, 1979; Woodward, 1979). Although the mating systems within these two types of social organizations are different, they both result in high variance of male reproductive success with particular males mating more than others. Harem group males have exclusive access to females within their groups, and territorial males of those equids with unstable relationships have exclusive mating access to females entering their areas. Furthermore, social organization and associated

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mating strategies appear to be adaptations of individuals to particular ecological restraints (Crook, 1970; Estes, 1966, 1974; Jarman, 1974; Kaufman, 1974; Klingel, 1974).

The objective of this paper is to provide an overview of some of the major aspects of the social organization and mating behavior of the feral asses on Ossabaw Island, Georgia. In contrast to the unstable relationships among feral and wild asses reported by Klingel (1972, 1977), Moehlman (1974, 1979), and Woodward (1979), the Ossabaw feral asses have extremely stable social groups, maintain territories, and have three basic mating strategies. This paper will also emphasize the effects of vasectomies used in this study as a population control procedure.

Study Area

Ossabaw Island, at approximately 110 km^2, is one of the largest barrier islands of Georgia. Ossabaw is currently a Heritage Preserve of the State of Georgia, and for many years has been maintained as a preserve by The Ossabaw Foundation for studies by biologists as well as by members of the arts and humanities community. Ossabaw is in a fairly natural state with the major habitats being forests (both _Pinus_ spp. forests and _Quercus_ spp., _Sabal_ spp., _Magnolia grandiflora_ mixed forests), salt marshes (_Spartina_ spp.), beaches, and some open grassland-pasture areas. Fresh water ponds are plentiful throughout the island. Ossabaw's climate is moderate with temperatures ranging from 4° to 13°C in winter and 27° to 37°C in summer. Generally, the warm climate and abundant rain on Ossabaw provide for very productive vegetation.

Subjects

Eleven asses (_Equus asinus_), reportedly direct descendants of Mediterranean asses, four males, six females, and one gelding, were introduced onto Ossabaw in 1965, By 1975, the original ass population had increased to 75, and it was apparent that population controls would be required. Due to the existence of Coggin's Disease among the equids on the island, exportation was not possible. A decision was made to vasectomize all the male asses to reach zero population growth and the eventual elimination of the asses from the island. The feral asses will remain free to live on Ossabaw and die natural deaths.

Methods

At the time of the decision to do the vasectomies, the feral asses were distributed throughout the rugged island terrain. Capture methods were those used for years to capture feral cattle on the island and were of various types. Roping from horseback was totally unsuccessful. Although horses proved faster than the asses during short chases, the asses were more durable than the horses and too evasive for close approach on horseback. Most of the feral asses were captured by fencing and plowing fields, and then planting millet to attract them. When the asses entered the fields to graze, the gates were closed behind them. Once the asses were enclosed in the fields, they were herded into loading corrals and transported to a 0.09 km^2 central holding pasture. Capture of all the asses required approximately three months.

When all the asses, both male and female, had been captured, two veterinarians from The Pennsylvania State University, Dr. John F. Kavanaugh and Dr. Lester C. Griel, Jr., established a field operating "room" on the island. All asses were aged by dentition, measured, and individually identified by ear tags. The males were then vasectomized, following procedures described by Kavanaugh and Griel (unpublished paper, in preparation). All of the feral asses were retained in the holding pasture for three months, during which time extensive behavioral data were obtained. After the three-month period, the asses were released from the holding pasture and again permitted free access to the island. The asses were observed continuously from May 1975 through August 1976, in January and February 1977, April and May 1978, March, May, and June 1979.

Collection of behavioral data was via focal-animal sampling, focal group sampling, sequence sampling, instantaneous and scan sampling (Altmann, 1974). Most data were collected utilizing focal group sampling techniques. Briefly, this procedure involved continuous observation and recording of specific interactions of each feral ass within a group during particular sample periods. When interactions were too frequent and/or too short in duration to permit written notation and data tabulation, the observer dictated the interactions, animal identities, and time periods into a casette tape recorder for later transcription.

Results

The original 11 feral asses, brought to Ossabaw in 1965, had increased to 75 by the end of 1975, which was the year this study began. Although a considerable increase, the population size in 1975 was much smaller than the 186 animals expected if the following assumptions had been met: (1) the sex ratio at birth is 50:50, (2) females reach puberty at two years of age, (3) all sexually mature females give birth to one offspring every year, and (4) there are no abortions or deaths (Fig. 1). Since the actual population size was much less than the theoretical population size, some or all of these assumptions were not met. Naturally, the number of abortions and deaths were not zero. However, deaths and abortions have not been frequent since observation began. The most likely assumption not met is number (3): all sexually mature females give birth to one offspring every year. However, during this study some females did give birth every year that sexually intact adult males were available for mating.

The population growth after 1975 was much slower than predicted, primarily because of the vasectomies. Five foals, from mothers impregnated prior to the vasectomies, were born in 1976, the year following the vasectomies. No foals were born in 1977. However, eight foals were born in 1978 due to mating of young, sexually intact males born after the vasectomies were performed. These young, sexually intact males were not expected to mate so early for reasons explained later in this paper.

Population Age and Sex Composition

The ages of the feral asses in 1975 ranged from less than one year to 13 years. Since fewer foals were born after 1975 than before, the population age structure shifted towards older animals. In 1975, most of the asses were less than five years old, and the proportion of animals in this age group has steadily declined from 81.3 percent in 1975, to 67.4 percent in 1976, 49.9 percent in 1977, and 34.8 percent in 1978 (Fig. 2). The sex ratios were 92 males:100 females in 1975, 86: 100 in 1976/1977, and 87:100 in 1978 (Table I).

Group Size and Composition

The feral asses were organized into eight to 11 relatively stable groups (nine groups were present during the majority of this study) which ranged from four to 22 asses per group. Three basic types of groups were present. Type I groups were those with one adult male, one to several adult females and their foals. Type II groups contained a dominant adult male, one to several subordinate adult males, and several adult females with foals. Type III groups were bachelor groups composed of all adult males. Age classes were identified following the procedure used by Moehlman (1974). Adults were two years old or older, juveniles one to two years old, and foals less than one year old.

Type I group harem males (mean age 7.0, range three to 13 years) and Type II group dominant males (two dominant male asses were two and eight years old; the two-year-old was eventually replaced by a six-year-old) were generally older than Type II subordinate males (mean age 3.2, range two to six years) and intermediate to Type III bachelor males (mean age 3.6, range two to 12 years).

Territoriality

Each of the eight to 11 groups of asses stayed in exclusive, well-defined areas. Type I and Type II group areas were defended areas, or territories (Noble, 1939). The sizes of these territories were small to moderately large and varied from 0.7 to 5.0 km^2 ($\bar{x} = 2.0$ km^2, n=5) for Type I group territories, and were 4.1 and 5.1 km^2 ($\bar{x} = 4.6$ km^2) for the two Type II group territories. The Type I adult males defended their territories from all other male intruders. Type II dominant males defended their territories with the aid of the subordinate males within their groups. Defense of the territories involved advertisement of their locations by the asses via regular braying, and at times vigorous fights and chases of intruder males by resident male(s) occurred. The asses of Type I and Type II groups stayed well within their territories and generally avoided the territory boundaries between their own and adjacent groups.

In contrast, the two Type III bachelor male areas (2.2 and 18.8 km^2, $\bar{x} = 10.5$ km^2) were not defended. These areas might best be described as home ranges. Also, groups of bachelor males often left their areas and traveled long distances into neighboring Type I and Type II territories.

Mating System

The male feral asses had three basic reproductive strategies. Type I adult males, being the only male in their harem groups, maintained exclusive mating privileges with their females. In contrast to Type I males, Type II dominant males were often challenged by subordinate males within their group for access to estrous females. The subordinate males assisted the dominant male in protection of group females from foreign males, but also attempted to mate females in estrus. The dominant male attempted to defend estrous females from the sexual advances of subordinate males, and, although he had greater access to and mated more often than did subordinate males, subordinates did sometimes gain access to estrous females. For example, during a nine-month observation period, one Type II group dominant male performed 53.3 percent of all the sexual mounts. The other five subordinate males in the group performed 18.3, 16.7, 11.7, 0.0, and 0.0 percent of the sexual mounts. Similarly, the dominant male attained 46.7 percent of all the ejaculations observed during the nine-month period as compared to 13.3, 20.0, 20.0, 0.0, and 0.0 percent of the ejaculations attained by the subordinate males. The dominant male's sexual advances were interrupted by the subordinate males 18.9 percent of the time, while subordinate males were interrupted by others 54.2, 24.1, and 30.8 percent of the time (two subordinate males were observed to make no sexual advances and hence, are not recorded here). The dominant male performed 48.6 percent of the sexual interruptions, and the subordinate males performed 20.0, 28.6, 0.0, 0.0, and 0.0 percent of the sexual interruptions. Occasionally a group female interrupted the sexual advances of males toward her adult daughter.

Type III bachelor males usually did not have access to estrous females within their own areas. However, groups of bachelor males often left their areas and traveled long distances into Type I and Type II group territories. Once discovered by the resident Type I or Type II male(s), the bachelors were usually chased from the territory. However, on occasion the bachelor males over-powered resident males and attained access to the females. When the bachelor males did gain access to an adult female, they attempted to drive her away from the resident males and mate her, regardless of whether the female was in estrus or not. Although there were dominance relationships among the bachelor males, the bachelors did not mate in the organized manner of Type I and Type II group males. Instead, the bachelors continuously struggled and fought among themselves for access to the female. The bachelor matings are best described as "gang rapes," for often the female was mounted simultaneously by two or more bachelors and mated by each bachelor in succession despite the female's struggles to get away.

During a 12-month observation period, asses of one of the two bachelor male groups attained access to neighboring group females only once. However, one female and her foal stayed within a bachelor group's area throughout this 12-month period, after which she joined a Type I group. Generally, none of the bachelors had a large advantage over the other bachelors for access to or mating of a female. The percent of total sexual mounts attained by each of the bachelors during the 12-month period ranged from 0.0 to 19.0 percent. Similarly, the percent of the total number of ejaculations achieved by the bachelors ranged from 0.0 to 28.6 percent. The bachelor male's sexual advances were interrupted from 10.0 to 75.0 percent of the time, and most of the active sexual interruptions were performed by only a few of the bachelor males.

Group Emigration-Immigration and Formation

Over a period of four years, there were some changes in the compositions of the ass groups. These changes were usually due to the onset of sexual maturity in young or to defeat of adult males. Generally, young males left their mothers by the age of two years and eventually joined one of the bachelor male groups. In two cases during 1975 to 1979, Type III group bachelor males cooperated with one another in order to over-power Type I and Type II group males and "steal" females. Once having acquired the females, the bachelor males established a new territory, and this led to the "birth" of a new Type II group. In one of the two cases, these new Type II group males were observed to fight among themselves and were, one by one, excluded from the area until only one male remained with the females, thus becoming a Type I group. In the other case, the acquisition of females and formation of the new group and territory were not observed. However, after a period of one year without observation, a former bachelor male was found alone with six females in a new area.

Female young usually stayed with their mothers much longer than did male young. Some females as old as four years were seen still with their mothers. Old as well as young males displaced from Type I and Type II groups joined one of the bachelor groups.

Discussion

The Ossabaw feral asses were vasectomized as a humane procedure for the eventual total elimination of the asses from the island via zero population growth and natural mortality. The primary objective of this study was not to evaluate the use of vasectomies as a procedure for population control. However, the use of vasectomies as a population control procedure may be of interest.

The vasectomies performed on the Ossabaw asses have not had a major effect on the fundamental aspects of the asses' overall behavior and social organization. The vasectomies performed in 1975 reduced the population growth rate as desired. Since they were not fertilized during estrus, the females continued to cycle on a regular basis, and this, of course, did increase the number of matings. However, there seemed to be no apparent difficulty or undesirable problems associated with the increased number of matings within the Type I and Type II groups.

There was one major difficulty encountered with the vasectomy procedure used on the Ossabaw asses. Normally, the female asses rejected their older young when the females gave birth to a new foal. The male young stayed within the group until about two years of age when sexual maturity was reached. At sexual maturity, the young males attempted to mate females within their groups, and the Type I or Type II group adult male(s) became very aggressive toward the young, eventually forcing them out of the group. The young males then joined the bachelor groups.

In contrast to the normal exodus of young males from Type I and Type II groups into the bachelor groups, the males born after the vasectomies stayed within their natal groups much longer than expected. Since the females were not impregnated by the males after the vasectomies were performed, the mother asses did not give birth to new foals and continued to associate with their last born young. Hence, when the young males reached sexual maturity and began to exhibit sexual interest in estrous females of the group, aggressiveness of the Type I and Type II group adult males was tempered by the mothers protecting their young male offspring. Hence, group females were fertilized by the young males. This led to eight births in 1978. In some cases, the mothers of young males were fertilized. When these mothers foaled, the older male offspring were rejected by their mothers and were eventually forced from the group by the other adult male(s).

The social organization and mating system of the feral asses could have been used to implement a population control procedure now that it is known that the vasectomies did not affect the asses' social organization and mating system. Since Type I group males usually have exclusive mating access to their harem females (even after the vasectomies were performed), it is reasonable to expect that vasectomies (but not castrations) on only Type I males and Type II dominant males would have resulted in a reduction of population growth. The vasectomized Type I group males and Type II group dominant males would eventually have been replaced by sexually intact males, and some intact subordinate males would also successfully mate. However, overall the number of births would have been reduced until the vasectomized males lost their privileged positions to other males. The Ossabaw groups remained extremely stable in composition from July 1975 through August 1976. By 1978, however, enough changes in group compositions had occurred that population growth would probably have again increased substantially had the original Type I and Type II dominant males been the only males vasectomized.

The stable social groups of the Ossabaw feral asses contrasts with other populations of asses. Klingel (1977), reporting on the African wild asses (*Equus africanus*) of the Danakil Desert, Ethiopia, and the Asiatic wild asses (*E. hemionus*) of the Karakum Desert in Turkmenia, USSR; Moehlman (1974, 1979) reporting on the Death Valley feral asses (*E. asinus*); and Woodward (1979) reporting on the Chemehuevi Mountain feral asses (*E. asinus*) in California, found no stable social groups other than mother-offspring pairs in their subject populations. Woodward also noted, however, that stable groups of yearling female and young male asses were present in her study group.

The defended territories of the Ossabaw asses are also in contrast to the large nonexclusive home ranges and territories of the asses studied by Klingel (1977); Moehlman (1974, 1979); and Woodward (1979). The Ossabaw Type I and Type II group territories were defended, exclusive areas and were much smaller ($\bar{x} = 2.7$ km^2, range 0.7 to 5.1 km^2, n=7) than the areas reported for the other asses. Even the two Type III bachelor group home ranges on Ossabaw were relatively small (2.2

and 18.8 km^2) compared to those of the other ass populations. Klingel (1977) reported male territories ranging from 12 to 40 km^2 ($\bar{x}$ = 23.0 km^2, n=7) for the African wild asses, and similar or even larger territories were estimated for the Asiatic wild asses. The African and Asiatic wild ass territories were usually nonexclusive areas, but they were defended when estrous females were nearby. Moehlman (1974) found the Death Valley feral asses to have home ranges that varied from 1.3 to 40.6 km^2 ($\bar{x}$ = 10.6 km^2, n=45). Woodward (1979) reported home ranges of 4.0 to 97.0 km^2 ($\bar{x}$ = 32.0 km^2, n=13) for the Chemehuevi asses, and found no significant difference between male and female home range sizes.

Moehlman (1974) and Woodward (1979) also found male territories that were relatively small in area. Five of the Death Valley male asses had small, non-overlapping territories ranging from 0.80 to 2.25 km^2 ($\bar{x}$ = 1.62 km^2, n=5) which were occupied seasonally, March through August. These areas, like the territories reported by Klingel (1977), were nonexclusive areas. Woodward (1979) reported one male that defended an exclusive territory of 0.5 km^2 from June through August. The territories of the Death Valley and Chemehuevi male asses, although smaller than the Ossabaw ass territories, were only occupied seasonally. In contrast, the Ossabaw asses occupied their territories throughout the year.

The mating system of the Ossabaw asses differs from the mating systems of the other asses studied. Adult females were guarded and exclusively mated by particular males in the Ossabaw Type I and II groups. These females remained within the same groups and territories for years and hence mated the same males for numerous years. In contrast, African wild ass males attempted to mate females that passed through their territories (Klingel, 1977). Similarly, Death Valley and Chemehuevi territorial male asses exclusively mated females entering their territories (Moehlman, 1974, 1979; Woodward, 1979).

Nonterritorial males did attempt to mate in all four of the ass populations discussed here, as one might expect. However, such matings were usually so chaotic, with numerous males competing for access to an estrous female, that mating attempts were often unsuccessful. Ossabaw Type III group bachelor males seldom had access to females and when they did, they fought so much among themselves and with territorial males for access to estrous females that they seldom mated successfully. Type II subordinate males who fought among themselves and with the dominant males also were relatively unsuccessful at mating. Klingel (1974), Moehlman (1974), and Woodward (1979) described mating attempts by nonterritorial males as chaotic and relatively unsuccessful as compared to the uncontested, exclusive matings by territorial males within exclusive as well as nonexclusive territories. Moehlman (1974, 1979) recorded a higher frequency of matings while estrous females were on nonterritorial areas than when they were on territories. Although Moehlman was not able to determine the relative reproductive success of territorial versus nonterritorial Death Valley males, nonterritorial mating seems to be a relatively more successful mating strategy for the Death Valley asses than for the Ossabaw asses, African wild asses, and Chemehuevi asses.

The differences in social organization, territoriality, and mating system between the Ossabaw asses and the other asses is very likely influenced by the two types of habitats occupied by the asses, as suggested by Moehlman (1979) and Woodward (1979). Ossabaw Island has abundant vegetation and plentiful rainfall. The African wild asses, Death Valley asses, and the Chemehuevi asses all inhabit desert areas. The abundant vegetation on Ossabaw is adequate to support the stable groups of asses in their relatively small territories. The territories, being small, are defendable by the resident male(s). In contrast, larger areas are needed in the desert habitats to support the asses on sparse vegetation and limited water. The cost to the male asses to defend such large areas is evidently too high in these desert populations. Resultantly, nonterritorial mating is generally more frequent in the desert populations than in the Ossabaw population. When territories are established by the desert males, the areas are often nonexclusive and seasonal.

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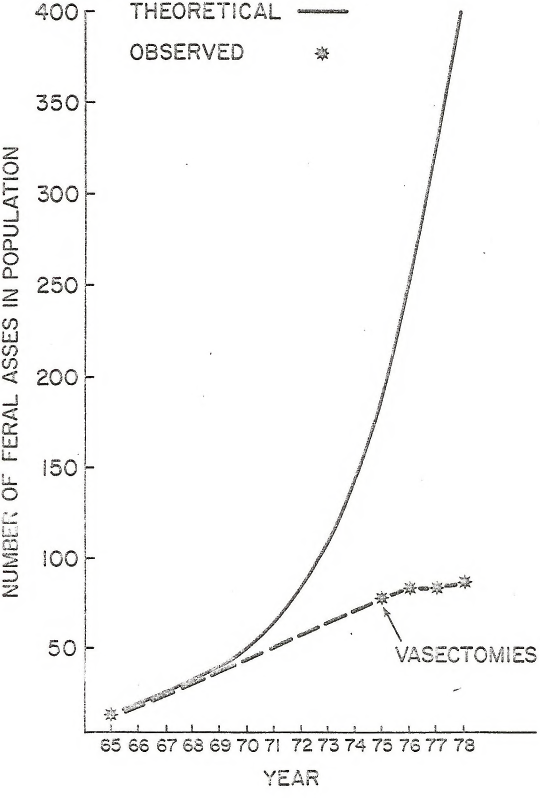
Table 1. Age and sex composition of the feral asses at the end of each year of observation.

	1975			1976			1977			1978		
Age (Years)	♂	♀	% Age Class	♂	♀	% Age Class	♂	♀	% Age Class	♂	♀	% Age Class
<1	3	7	13.3	1	4	6.2	0	0	0.0	3	4	8.1
1	4	5	12.0	3	7	12.5	1	4	6.2	0	0	0.0
2	11	5	21.3	4	5	11.2	3	7	12.5	1	3	4.6
3	8	6	18.7	11	5	20.0	4	5	11.2	3	7	11.6
4	3	9	16.0	8	6	17.5	11	5	20.0	4	5	10.5
5	0	3	4.0	3	9	15.0	8	6	17.5	11	5	18.6
6	2	3	6.7	0	3	3.8	3	9	15.0	8	6	16.3
7	0	1	1.3	2	3	6.2	0	3	3.8	3	9	14.0
8	1	0	1.3	0	1	1.2	2	3	6.2	0	3	3.5
9	1	0	1.3	1	0	1.2	0	1	1.2	2	3	5.8
10	1	0	1.3	1	0	1.2	1	0	1.2	0	1	1.2
11	0	0	0.0	1	0	1.2	1	0	1.2	1	0	1.2
12	1	0	1.3	0	0	0.0	1	0	1.2	1	0	1.2
13	1	0	1.3	1	0	1.2	0	0	0.0	1	0	1.2
14	0	0	0.0	1	0	1.2	1	0	1.2	0	0	0.0
15	0	0	0.0	0	0	0.0	1	0	1.2	1	0	1.2
16	0	0	0.0	0	0	0.0	0	0	0.0	1	0	1.2
Total	36	39	99.8	37	43	99.6	37	43	99.6	40	46	100.2
Ratio	92:100			86:100			86:100			87:100		

Figure 1. Theoretical versus observed Ossabaw feral ass population sizes and growth. Asterisked points represent observed population sizes at the end of each indicated year.



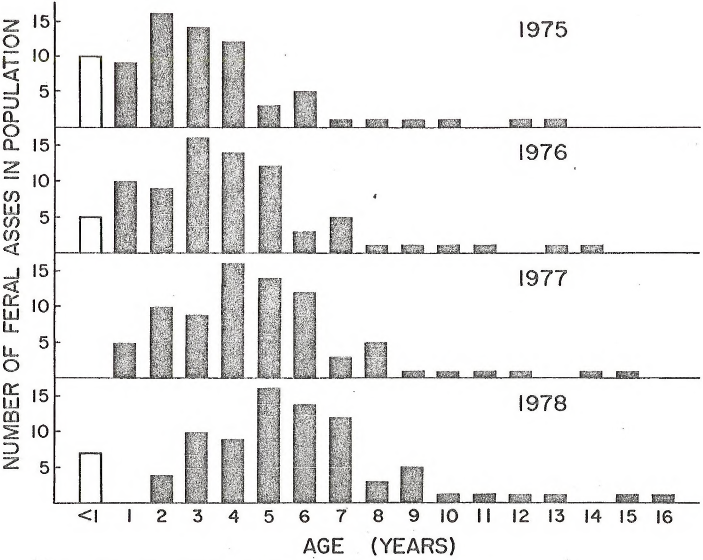


Figure 2. The number of feral asses in the Ossabaw population versus their ages in years for each year of observation, 1975-1978.

Quantitative Aspects of Elimination Behavior in Feral Stallions

John W. Turner, Jr., Anne Perkins, Els Gevers, and Jay F. Kirkpatrick
Department of Biological Sciences, Eastern Montana College, Billings

Abstract

Various behaviors exhibited by feral stallions, including herding, grooming, aggression, copulation, and elimination behavior were studied. Preliminary data based on 68 hours of direct observation of 73 horses comprising 17 different bands indicated that the only behavior which occurred with high frequency and was readily observable and quantifiable was elimination behavior. Stallion elimination behavior was defined as the behavioral response of stallions to urination and/or defecation made by other horses and simultaneously noticeable by the stallion. This behavior was quantitated for frequency by dividing frequency of responses by frequency of eliminations (elimination behavior quotient, EBQ) and quantitated for intensity by subdividing the overall response into sequenced parts, with the display of the complete sequence representing the greatest intensity. Results are based on 454 hours of direct observation of 102 horses comprising 27 groups between January 1976 and October 1978. Elimination behavior was not exhibited by mares or immature animals. Stallions responded to elimination by immature animals in only four of 172 occurrences. Behavioral response to elimination by mature mares varied markedly with time of year. The incidence of response was greatest (80%) from April through July and lowest (0.01%) from November through February. In May and June, the peak of the breeding season, stallions responded to 93% and 89% of the eliminations, respectively. The intensity of response showed an annual pattern similar to that for the EBQ, with most complete response patterns occurring in May and June. Neither the frequency nor the degree of the stallions' behavior response was influenced by time of day or weather. The stimulus for seasonal changes in stallion elimination behavior is not known. However, correlative seasonal changes in stallion plasma androgens and mare plasma steroids have been observed, and the possibility of endogenous stimulus by androgens as well as exogenous changes in fecal constituents must be considered. Stallion elimination behavior appears to provide a useful index of behavioral changes associated with reproductive patterns in feral horses.

Behavioral Adaptation as a Factor in the Management of Feral Equids

George H. Waring
Department of Zoology, Southern Illinois University, Carbondale

Abstract

Management of feral equids, if success is to be realized, must be based around adaptive mechanisms and biological parameters of the species involved. Behavioral adaptations are among the important factors to consider. Poor management practices plus poor enforcement of regulations have historically been involved in the world-wide decline of equid populations. Man and livestock have persistently encroached on equid habitats. The tendency of free-roaming equids has been to avoid such competition and the problems associated with man. They have retreated to isolated areas; have remained wary of intruders; have at times shifted activity, social, and maintenance patterns; and have adapted to habitats scarce in food and water resources. Equids have survived because they are morphologically, physiologically, and behaviorally well adapted.

Although each species has its behavioral norms, flexibility in behavior exists. When preferred foods are not available, equids shift to other food items, such as to browse or aquatic plants. When water is not readily available, they drink less often and may walk great distances to reach a water source. Some even dig for water or for food. When harassed, they emigrate or alter their activity patterns. If herd composition, available space, resources, or other environmental characteristics are altered, the social structure, distribution, habitat utilization, and herd stability are among the factors also likely to change. For example, where dispersal is limited, resources are evenly distributed, and potential interactions are high, some feral horse herds have non-overlapping home ranges, and in some cases these areas may be defended territories. Furthermore, feral burros vary from being primarily solitary in sparse habitats to being highly social in luxuriant environments.

To maintain healthy herds, management programs need to work in harmony with the adaptive mechanisms and behavioral plasticity of the species. Adequate food and water are key resources and are fundamental to each home range. In certain regions, summer shade or winter shelter may be secondary factors important to habitat utilization. Habituation and training may be necessary before feral equids can be expected to circumvent new barriers or utilize new devices to reach food or water. Herd social stability, spatial requirements, and cyclic movement patterns, including dispersal, need to be accommodated in every management plan. Programs based on population disruption will undoubtedly fail. Feral equid management should be tailored to the well-being of each population as well as to each location and should avoid interfering with natural-occurring environmental safeguards.

Introduction

Of the populations that exist today of the domestic horse, Przewalski wild horse, African ass, Asian ass, Grevy's zebra, Burchell's or plains zebra, and the mountain zebra, some are legally declared "Endangered." Yet nearly all free-roaming equid populations face, or potentially face, threats to their existence. Population declines are widespread. The Przewalski horse may already be gone except in captivity. Poor management historically has been directly or indirectly involved in the loss of equids and their habitats.

To successfully manage animal populations, it is certainly important to consider adaptive mechanisms of the organisms involved. A broad view of related species is often helpful to understand any one species. Yet, it is not reasonable to expect that equids can be successfully managed following traditional management guidelines established for ruminants. Each species has different adaptive strategies. In this paper, I wish to especially emphasize behavioral adaptation and its relationship to management.

Problems Facing Populations

First let me review a few of the common problems facing equid populations and the response of the animals to those problems.

Over the last few thousand years, human settlements, farms, and livestock grazing lands have steadily spread across the former habitats of equids, forcing the herds to seek refuge in wastelands. It is reasonable to assume that most wild equids originally occupied far better habitats than they occupy today.

Przewalski horses (*Equus przewalskii*) occurred in historic times over the entire steppe and forest-steppe zones from central Asia westward (Heptner, 1961; Bökönyi, 1974). Hunting with increased colonization and tilling of the habitat reduced the distribution of Przewalski wild horses to the edge of the Dzungar wasteland of northern China. By 1940 the distribution had dwindled to a small zone on the China-Mongolia border (Bannikov, 1967a). Historically, the herds migrated between the Mongolian border in winter and the Dzungaria in summer (Dovchin, 1961). Recent reports, however, suggest the bands are on the Chinese side of the border in autumn-winter and on the Mongolian side in spring and summer (Tsevegmid and Dashdorj, 1974).

Both Mongolia and China forbid shooting of Przewalski horses, but problems continue. The range has little water and vegetation (mostly halophytes). Cattle breeders moved their herds into the area after 1950 and occupied all the open springs. The already small wild horse population showed an immediate drop (Bannikov, 1961). Settlement of the region continues. Subsequent observers generally fail to find the remnant horses or see, at most, up to 11.

The Mongolian kulan (*E. h. hemionus*), like the Przewalski wild horse, has been protected from hunting since 1926 in the Mongolian People's Republic. Nevertheless, distribution and available resources have changed with greatly increasing human and livestock populations.

Kulan herds have moved eastward into the Galbyn and Borzorghiin deserts of the East Gobi province where none were found 25 years ago (cf. Andrews, 1933; Tsevegmid and Dashdorj, 1974).

In 1919, shooting of wild Asian asses was prohibited in the Soviet Union. At that time the Russian onager (E. h. onager) population had dwindled to two distinct areas, in eastern Turkmen as well as around the Balkhash and Zaysen Lakes in Kazahh. Harsh winters and persecution by man continued a population decline. By 1936 the onager population in Kazahh was gone. The Turkmen population had declined to the region of Badchyze, and in 1941 the Badchyze Reserve was established for the remaining 300 onagers in the Soviet Union. At first, protection was difficult to accomplish and by 1953 the population was down to about 120. Fortunately from 1955-1960, onager immigrated into the Reserve from Afganistan. And by 1964 the population had stabilized at about 700 (Bannikov, 1967b). Onagers move to and from the Reserve seasonally.

The kiang (E. h. kiang) is found only on the high Tsinghai-Tibet Plateau of China above the forest zone. The animals have been granted full protection; yet, poaching is a problem. Hunters eagerly seek kiang hides and flesh. In the last few decades, the kiang population has also had to compete with cattle for grazing areas (Volf, 1972).

These are only a few of the examples that could be cited. Zebra populations and other wild as well as feral equid populations have known or are experiencing similar population threats.

Thus equid populations are faced with problems and have drastically declined. In many cases, free-roaming equids are increasingly faced with a loss of their food and water resources on their already sparse ranges. Their tendency has been to avoid competition with man and his livestock, but today there are few remaining retreats. Hunting pressures, severe weather, drought, and disease remain as further vexing problems.

Equid Adaptations

Throughout the advance of man, equids have shown behavioral adaptation by retreating to isolated areas; by remaining wary of intruders; by shifting activity, maintenance, and social patterns; and by adapting to habitats scarce in food and water resources.

Yet, equids are well adapted. They can cope with many environmental problems. In general, they are morphologically adapted as fleet-footed grazers capable of moving relatively long distances to satisfy their biological needs. (See Hassenberg, 1971; Klingel, 1972; and Waring et al.,1975,for an ethological review).

Physiologically equids are adapted to digest a wide variety of plant materials. Their cecal digestion, high intake, and rapid food passage enable them to maintain themselves on a high fiber/low protein diet (Janis, 1976). When grasses or grass-like materials are not available they shift to other plant materials, including browse and aquatic plants. Seasonal shifts in feeding and feeding sites often occur. They thus cope with scarce food resources and also limited water. They also tolerate extremes in ambient temperatures as well as snow cover (cf. Klingel, 1977; Salter and Hudson, 1979; Woodward, 1979).

Equids remain well oriented in their environment, establish trails, and maintain themselves in relatively stable home ranges. They are shy and watchful of potential dangers. Their social patterns range from solitary, territorial traits to highly social, non-territorial groupings (Klingel, 1975).

Young equids are relatively precocial and mobile; yet, they require maternal protection and care for several months. Social development extends over at least one year and includes play with peers or mother. Although sexually mature as early as one-two years, breeding is often delayed a year or more by social and environmental factors.

Social structure centers around one or more adult females. Social attachments can be strong and may involve more than just close relatives. Associated with each social unit, especially in prime habitats, is commonly an adult male who generally is in an alpha, but not necessarily leadership, position. Bachelor individuals or groups can also exist.

Males compete for females and, depending on the environmental context and to a lesser degree on the species, the male may maintain a territory per se, or a harem, or both.

Within certain cyclic limits, the size of wild equid populations stabilizes, with recruitment and mortality becoming equal over time.

Behavioral Plasticity

Although each species has its behavioral norms, flexibility in behavior exists. Behavioral plasticity certainly occurs in equids, and it is because of such plasticity that they have survived so long.

When preferred foods are not available, equids can shift to other food items. When water is not continuously available, they can space their drinking so as to feed many kilometers away and drink once a day or even less often in some cases (e.g., Bannikov, 1961). Like Grevy's and mountain zebras, some feral horses dig for their water (Welsh, 1973, 1975). When seasonal abundance of resources occurs, equids capitalize on those supplies and shift from what before seemed to be established routines.

When harassed by man, insects, or other environmental factors, they shift their diet behavior patterns to become active at more tolerable times and places.

When sex or age ratios are altered, or when space or resources are limited, social behaviors including social structure and reproduction may be altered. In Tyler's (1972) study in the New Forest, nearly all colts and many fillies were removed from their mothers in the first autumn or winter. Group size remained small; 60% of the groups consisted of one adult mare with recent offspring. Less than 12% had three or more mares. The limited number of stallions copulated with mares belonging to many different groups, and long-term association with any one band was usually disrupted by removal or translocation by man. Although most stallions tended to associate more with one band, some stallions remained single. In contrast, Stebbins (1974) observed horses under somewhat similar circumstances with limited stallions, except social structure was not routinely disrupted by man. In this case, band size was much higher, averaging 20.8 horses per stallion group and 6.4 for bands not containing stallions. Unlike the New Forest situation, in this study none of the stallions remained single.

Management Implications

Now, what does behavioral adaptation have to do with the management of feral equids?

First, it is important to realize that feral equids need and utilize space. How much space will depend especially on the quality of the habitat. Within the habitat, water and food are the two key resources. Since equids can utilize a variety of plants for food, water usually becomes the focal point of home ranges, at least in arid habitats. Where water is scattered and abundant, prime feeding sites become the center of activity. Secondarily, shelter becomes a factor in herd distribution and habitat utilization. Shelter is especially important in harsh winter environments; yet, shady resting sites are often sought in summer.

Although feral equids undoubtedly have innate responses to certain environmental stimuli, they exhibit a keen ability to learn. For example,they are wary and avoid noxious stimuli (e.g., Welsh, 1975); yet, they can habituate to recurring non-adverse stimuli (e.g., Keiper, 1976a, 1976b). Horses have performed well in discrimination tasks, delayed response paradigms, and memory experiments (Waring et al., 1975; Fiske, 1976). Yet, detour problem-solving is a weakness and can well be important in management. Equids are not quick to search for detour routes around barriers. Thus the animals may need to be taught where to find gates and pathways to water and other resources whenever new barriers are erected. Habituation and training may also be required when man-made watering or feeding devices are employed.

Once familiar with their environment, free-roaming equids establish relatively stable home ranges. The animals subsequently demonstrate a homing tendency and return to their previous range when moved or displaced by man. Regional translocation of animals is for the most part not practical. Unfamiliarity of physical and social surroundings is stressful and concomitant physiological and behavioral responses are to be expected (Geist, 1978).

When separated from herd companions, there is a strong tendency for individuals to return to their social unit when displaced from that group (e.g., Tyler, 1972). This tendency varies between species, environmental context, and also with age and reproductive status. Nevertheless, sociality is important to all equids, at least in some stage of their life cycle, and management activities must anticipate this. Assumptions that redistribution of herd composition can be accomplished may be ill-founded.

Harassment, such as by motorized vehicles, can lead to dispersal movements and physiological disruptions. Furthermore, new structures or noxious stimuli in their environment may cause avoidance of areas previously used. For example, Welsh (1975) found seismic testing caused major changes in the horse distribution on Sable Island.

Emigration and immigration can occur to other factors as well. As the reproductive condition of equids change, especially in young adults of either sex as well as in adult males, dispersal or alteration of social patterns often occur. Such movements should be expected and permitted if dynamic homeostasis of the population is to be realized.

Temporary dispersal from social units also occurs. Mares frequently separate from their group at the time of parturition and may not rejoin previous companions for several days. Juvenile equids also are known to temporarily leave their social unit to join other peers in grooming or play activities. Thus occasional wanderings are normal.

Removal or loss of herd members can create serious disruptions to social units. On Sable Island, for example, the loss of a herd stallion in winter places the rest of the social unit in jeopardy especially if a new yet inexperienced male moves the herd into areas with poor shelter and poor food quality (Welsh, 1973). Culling activities can destroy behavioral stability and lead to herd instability.

Scarce resources can also lead to dispersal of equids, or to overuse of certain areas, for example, when water is the limited resource. Cyclic use of the habitat with accompanying movements can be expected in equids, especially in arid regions. Barriers or harassment can obstruct such environmental safeguards and can therefore lead to habitat degradation.

It now appears that space and resource distribution are key factors involved in major shifts in social organization. On island habitats, for example, where dispersal is limited, potential interactions are high, and resources are evenly distributed, some feral horse herds have non-overlapping home ranges (e.g., Zervanos and Keiper, 1979) and in some cases may become territorial and repel intruding horses (Rubenstein, 1978). Feral burros also have been observed to alter social structure--being primarily solitary in one habitat (Moehlman, 1974; Woodward, 1979) and highly social in another (McCort and Graves, 1979).

Thus in any management program, the behavior or perhaps I should say the behavioral flexibility of equids is very important. Management programs cannot assume that diet, or the home ranges, or the social structure, or the habitat utilization patterns, or the rhythmicity, or the social groupings of free-roaming equids will remain constant. As the environment changes (whether by fences, alteration of water holes, livestock grazing, climatic changes, fire, harassment, and so on) so may also a change be noted in the behavior of the equids. Planning must encompass and yet not be over reactive to such adaptations.

Feral equid management, pursuant to the goals and objectives of the Wild Horse and Burro Act of 1971, will only be successful if the physiological as well as behavioral well-being of the equid populations are maintained. Management based on population disruption will not produce healthy herds and thus will not be successful management. To be successful, management of feral equids must work in harmony with the adaptive mechanisms of the animals. Management must also be tailored to each location. Thus management programs need flexibility to stay abreastof regional differences and equine behavioral flexibility.

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The Varying Role of the Male in Feral Horses

R. H. Denniston
Department of Zoology and Physiology, University of Wyoming, Laramie

Abstract

For the past four years a study has been conducted on the Red Desert of Wyoming concerning the role of males in multi-male bands and multi-band herds. During a colt's life he is barely recognized as playing a male's role. From the age of two-three, his role begins to emerge, at which time he usually joins a bachelor group or becomes a loner. At the age of three-four, the male associates with a mixed-sex band without constant status. With age comes a decrease in dominant status. In contrast to other equid systems, the multi-male organization could possibly represent an R strategy, whereas the multi-band herd organizational scheme must be emergent and represent a new strategy for large numbers of equids.

Introduction

The ungulate traditionally shows a sexual dimorphism in behavior. The male shows much more agonism, intra- and interspecifically. His prototype might be the bull elk or ram bighorn sheep, where a large amount of the rut is spent in sexual combat. In both, threat, ritualization, dominance-subordination, and submission play well recognized roles. The dominant male is a harem master, rounding up, defending, and doing most of the breeding with his group of females--a male chauvinist par excellence.

So it has seemed to be with equids, and four years ago when we started to work with feral horses this is what we looked for (Denniston and Miller, 1978; Miller and Denniston, 1979). To some extent it is what we found, but two sorts of exceptions appeared: multi-male bands and multi-band herds. Multi-male bands may represent a trade-off by a dominant male for band defense by subordinate male band members. Multi-band herds are an exception because they may include or have attached to them single males or bachelor groups. Such herds are groups of bands with a common home range and common movement patterns, organized into a social structure with considerable mutual recognition and compatibility.

Agonism and Dominance

Male-male conflict occurs in many situations. Some typical encounters are presented in Table I. Most often the instigator is a band male or a satellite male of a multi-male band. More rarely it may be the male of a small band; and occasionally, under crowded conditions, it may be a dominant female. The resource competed for is often related to band integrity: a female or a foal. It shifts from such resources to water, in the latter part of the summer. The recipient is most often an interloping male, either a bachelor or one from another band. The whole

will utilize the scarce water supply with the band. As the mares of his band come on heat, he may share them with little friction from other band stallions, either during the same day or doing all the breeding for two or three days and then none for a similar period. He will be increasingly recognized by other band stallions in the herd. Almost imperceptibly he may gain a dominant position in his own band and in relation to other bands.

Just as gradually, he will lose his dominant status. If the other stallions in his band are much younger, the band may start losing mares and their foals. The band may break up completely and the previously dominant stallion become a loner, sometimes tolerated briefly by other bands in the herd.

Adaptiveness of the Male Role

Such a system does several things for the overall population: (1) it insures that most breeding is usually done by the most rugged males; (2) at the same time it is usually only distantly related females with whom they breed; (3) a given female may be bred by a variety of males -- all with a high degree of fitness. The efficacy of this system is demonstrated by the thriftiness, generally good configuration, variety of coloration of the horse population on the Red Desert of Wyoming.

Our findings as to how a male may acquire a band are similar to Welsh's. His Sable Island ponies were also exposed to rigorous winters when bands mingled. He reported no multi-male bands or multi-band herds. Keiper in 1976 reported some multi-male bands. What he describes as co-dominance in bands of young horses is like our shifting dominance in mixed bands.

Both Tyler's (1972) New Forest ponies and Imanishi's (1950) Toimisaki horses had the adult males culled from the group, leading to a very low male/female ratio and little male-male competition.

These horses do not fit either Klingel's (1969, 1974, 1979) harem category nor his territorial male type. In the Pleistocene, horses showed a great morphological radiation. Is it possible that we now have an equally great behavioral radiation?

Why is this system different from other equid systems? Klingel lists only two types: harems and territorial males (Klingel, 1969, 1974, 1979). Feral animals tend to revert toward the wild condition. Possibly Red Desert horses are only partly reverted toward a harem system. The multi-male organization may represent an R strategy in an expanding population. The relatively low foal loss reported by Miss Lee Boyd (Boyd, 1979) would be characteristic of R strategy. The super-band herd organization must be emergent and represent a new anti-agonistic strategy for large numbers of equids in contact with each other. In the somewhat parallel situation of zebra, different strategies have evolved.

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Table 1

Month	Instigator	Resource	Recipient	Special Circumstances	Agonistic Behaviors	Outcome
May	Band M	F (estrous)	Bachelor M	Bachelor approaches F in band.	Forefoot pawing, deep head-bowing, competition on stud pile	Interloper rejoins bachelor group.
May	Small band M	F from large band	Large band M		Arched neck threat, rearing	Small band M returns to its group.
May	Small band M	F from large band	F + 3-yr. M from large band	Herding by small band M of M and F for over one hour	Herding Head projecting	Small band M returns to own band.
May	Large band	Graze	Medium band	Move through each other grazing one-half hour	None	Separation of bands
May	Large band M	Estrous F (2-yr.-old)	M from other large band	M from other band mounts F. M from 3rd band interferes.	Rearing and striking	Breeding M driven off. F returns to own band.
May	Newly accepted M to band	Band integrity	Bachelor M, M from small band	New M goes out to incoming MM.	Challenges Arched neck threat Foreleg kick Neck bite Chase	Interlopers driven off.
May	Small band M	Band integrity	2 bachelors Newly accepted M from other band		Chase Fight	Interlopers driven off.
June	Band M	Band integrity	Foal	Foal wanders off.	"Snake" herding	Foal returns to band.
June	Band M	Band integrity	Former band MM	2 MM who lost FF over winter approach large band.	Chase	Interlopers driven off.
June	Band M	Estrous F	M from other band	Band M breeds F 3 times then strange band M breeds her.	None	Other band M returns to band.
June	Band M	Band integrity	Other band M	Strange M herds foal back to foal's band, is challenged by M of that band.	Rush Chase	Herding M returns to own band.

Table 1 (continued)

Month	Instigator	Resource	Recipient	Special Circumstances	Agonistic Behavior	Outcome
June	Large band M	Dominance	Small band M	Small band approaches large band.	Rear Challenge Small band M bows deeply, extends foreleg.	Small band M retreats.
July	Band M	Band integrity	2 FF from band	FF started away from water, trailing strange band.	Arched neck threat "Snake" herding	FF return to own band.
July*	Band M	Water	9-member band	Many bands attempting to drink	Arched neck threat Rearing Shouldering	Band remains on water.
July	2 Band MM (same band)	F, 2-yr.	M, 3-yr.	M and F herd foal back to original band. 2 MM from that band challenge 3-yr. M.	Chasing Arched neck threat Rearing	3-yr. M goes off with F.
July	Band M	Water	Bachelor M from 5 MM	Crowd at water	Arched neck threat	Band stays on water.
July	Dominant F	Dominance	Other FF in band	Crowding around water	Chasing	---
July	Band M	Band integrity	M who had lost band; M from other band		Separated M marks stud pile; band M marks then arches neck. Band M rears with M from other band.	Separated M leaves.
July	2 Band MM	Water	5 Bachelors	Crowd at water	Arched neck threat Chasing	Band stays on water.
August	Band M	Band integrity (Water?)	Bachelor		Bachelor marks stud pile. Band M marks on top then chases bachelor; LEADS him away from band.	Bachelor led off.
August	2 Bachelors	Dominance	2 Other bachelors		Alternate fighting on hind legs	Move off together in group.

*Repeated by different band males throughout dry period

Avoidance, Maze Learning, and Social Dominance in Ponies

Rebecca Rudman, Ellen Haag, and Katherine Albro Houpt
Department of Zoology, University of Oklahoma, Norman

Abstract

A herd of ten grade ponies was used in a three-phase study conducted at Cornell University's Equine Research Park in Ithaca, New York, in an attempt to correlate dominance, aggression, and learning ability. Dominance was determined in both a group and a paired situation. Threat gestures employed by each pony during the paired dominance trials were also recorded and given numerical values depending upon degree of intensity, so that the pony with the highest total score was considered the most aggressive. Two learning experiments were conducted. The first was a shock-avoidance experiment, in which the ponies learned to jump a low barrier to escape a mild shock. The second was a single choice-point maze learning experiment. Physical parameters recorded included height, weight, age, and sex. The paired dominance rank showed a highly significant positive correlation with the aggression rank. The dominance tests also correlated significantly with each other, suggesting that both methods are suitable for determining dominance. Significant correlations were found between maze rank and ranks on performance in the shock-avoidance study. These results imply that long-term learning and learning permanence are related. Better learners in a classical avoidance conditioning situation employing an aversive stimulus also tend to learn more quickly in a maze learning, or operant, conditioning situation with positive reinforcement. No correlations were found between learning ability and dominance or aggression, and none of the physical parameters correlated significantly with the results of these three tests.

Introduction

For many animal species, the ability of an individual to learn is important for survival. Learning has been defined as the adaptive modification of behavior (Lorenz, 1973, cited by Eibl-Eibesfeldt, 1975). The behavior of an animal may be modified through one of several different processes. These include habituation, conditioned learning, reinforcement learning, latent learning, and insight learning (Eibl-Eibesfeldt, 1975). Two of these five learning processes, conditioned learning, or classical conditioning, and reinforcement learning, or operant conditioning, have been investigated extensively. A number of studies on these forms of learning have been done with domestic animals. Shock-avoidance learning, a type of classical conditioning, has been tested in pigs (Karas, Willham, and Cox, 1962; Willham, Karas, and Henderson, 1964; Kratzer, 1969) and dogs (Whatmore, and Kleitman, 1946). Studies have also been conducted on maze learning, a form of operant conditioning, in swine (Wiekert and Barr, 1966; Hammell, Kratzer, and Bramble, 1975), cattle (Wieckert et al., 1966; Dickson, 1967), and horses (Kratzer et al., 1977).

Another important aspect for survival in a number of species is the maintenance of a herd. Group living can provide many benefits to the members of the group, such as greater protection from predators and increased

reproductive success (Eibl-Eibesfeldt, 1975), but the constant close contact between individuals also leads to greater competition for resources. To preserve the cohesion of the group, a dominance hierarchy is often established, the more dominant animals of the hierarchy having first access to resources. The rank order is maintained by the use of threat gestures rather than actual fighting, and aggressive interactions are less likely to cause serious injury to herd members. Dominance hierarchies in horse herds have been described by a number of investigators (Montgomery, 1957; Tyler, 1972; Stebbins, 1973; Clutton-Brock, Greenwood, and Powell, 1976; Feist and McCullough, 1976) and the threat gestures employed by horses have been described as well (Montgomery, 1957; Tyler, 1972; Feist and McCullough, 1976; Houpt, Law, and Martinisi, 1978).

The purpose of this investigation was three-fold: (1) to determine whether position in a dominance hierarchy and level of aggressiveness are related, (2) to determine whether dominance rank is correlated with rank in learning ability, and (3) to determine whether there is a correlation between maze learning and shock-avoidance learning ability in ponies. Maze learning and shock-avoidance learning results were compared to see if the performance of the ponies was consistent for two learning tasks involving different motivations, sensory requirements, and motor abilities. Finally, the physical parameters of weight, height, and age were correlated with the results of the learning and dominance experiments. These variables have been correlated with dominance rank in previous studies (Montgomery, 1957; Tyler, 1972; Stebbins, 1973; Feist and McCullough, 1976; Houpt et al., 1978) with different results. Kratzer et al. (1977) examined the relationship of height and weight with maze learning ability in yearling Quarter horses, but we are not aware of any other studies concerning the relationship between learning ability and physical parameters in horses.

Materials and Methods

Ten grade ponies, six mares, two geldings and two colts were used in this study. All ponies were freeze-branded with identification numbers. Six of the ten ponies had cecal fistulas from a previous experiment.

Dominance tests

The primary test used was similar to that employed by Houpt et al. (1978) and consisted of a contest between two ponies (both fasted for 22 hours) over a bucket of sweet feed. The feed bucket was only large enough to enable one pony to eat from it at a time. It contained an amount of grain 25 percent less than the normal ration given to two ponies at a single feeding. The ponies were held at equal distances from the bucket and released simultaneously. One observer recorded the time spent by each pony in control of and/or eating from the feed bucket. Two other observers, each watching one pony, recorded all aggressive actions for that pony. Contests were run for 15 minutes or until all of the grain was eaten.

Each pony was tested with every other pony, a total of 45 pair combinations, and was used for only one test per day. The dominance hierarchy was based upon the number of times each pony was the dominant member of a contest. The pony that controlled the feed bucket for the majority of the time was considered to be dominant. In cases where the times were within one minute of each other the ponies were considered to be of equal dominance. The alpha (highest ranking) animal was dominant over the greatest number of ponies, the beta (second ranking) animal over the next greatest number, and

so on. In a case where two ponies were dominant over the same number of ponies, the winner of the contest between the two ponies in question was given the higher dominance rank.

An aggression rank was determined by computing the total aggression score for each pony in all contests. Aggressive actions were classified and assigned point values from one (mildest) to nine (most severe) as follows: (1) facial threat (turning of head toward opponent, ears back); (2) supplant (dominant animal causes subordinate to relinquish control of feed bucket with no obvious threat or physical contact); (3) head bump (as described by Montgomery, 1957); (4) threat to bite (ears back; mouth open, usually exposing teeth, and closed near opponent as if to bite; animal may lunge at opponent with head extended); (5) threat to kick (ears back; sudden pivoting of hindquarters toward opponent; animal may lift hind leg and/or swish tail); (6) strike (using forelimbs); (7) bite; (8) kick (using one or both hind legs); (9) chase (aggressor chases opponent, ears back, for more than three steps. The scoring system included all of the agonistic interactions observed. The ordering of interactions was based upon the series of acts that occur in confrontations between stallions (Feist and McMullough, 1976).

A second type of dominance test was run in which ponies were observed in a group for 20 minutes on three successive days. The ponies were fasted for six hours prior to the trials. On the first day, all ten ponies were turned loose in a paddock containing one bucket of sweet feed. Each time two ponies were involved in an agonistic interaction, as evidenced by any of the aggressive actions discussed above, their numbers were recorded and the winner of the interaction was indicated (e.g., 416>26). Only two ponies were successful in getting feed on this day. On the second day, these ponies were omitted from the group so that the lower ranking ponies would be involved in more interactions. On the third day, the third and fourth ranking ponies were also removed. Sufficient data were obtained on this day to assign a dominance rank to all ten ponies. The dominance rank was determined using the method of Schein and Fohrman (1955).

Avoidance learning test

A two-way shock avoidance apparatus similar to that employed by Karas et al. (1962), Kratzer (1969), and Hammell et al. (1975), was used. The 7.0 x 3.5 meter testing area was divided in half crosswise by a wooden pole set at 0.5 meters above the ground. The pole served as the obstacle over which the ponies jumped to avoid the unconditioned stimulus.

A pulsed buzzer of ten-second duration provided the conditioned stimulus (CS) and an electrical shock served as the unconditioned stimulus (US). Shocks were administered with a shock generator (Grason-Stadler, model E6070B) in conjunction with a 28-volt DC power supply set at 0.06 milliamps. Both shock and buzzer were controlled manually, and a stopwatch was used as the timer. A rubber belt held two electrode plates against a shaven area on both sides of the pony, posterior to its center of gravity. The electrical leads to the plates were tied to the top of the belt with slack allowed so that the plates would not be pulled out of position. Conductive electrode gel was applied to the plates prior to the start of a session. Intensity of the US was the minimal level of shock which produced a noticeable reaction in each pony and/or caused it to move forward. This level varied from 1.6 to 3.0 mA among the ponies. The determination of individual threshold levels was made to control for differences in sensitivity to shock among the animals. A similar procedure

for determining shock level was used by Whatmore and Kleitman (1946). The ponies were led over the jump six times before the avoidance test was begun to familiarize them with the testing situation.

One session of ten trials was given each day for ten days. A 30-second intertrial interval was employed for consistency. A trial consisted of presentation of the CS (the buzzer), followed in ten seconds by the US (the shock) if the pony had not jumped the barrier. The ponies stood about 1.5 meters from the jump and were held to prevent them from moving forward until the buzzer sounded, at which time they were released and permitted to move freely. A pony that failed to jump the obstacle during the CS was led over the jump as soon as the shock commenced. This differed from the experimental procedure of Kratzer (1969) and Hammell et al. (1975), whose animals escaped the shock without assistance. As soon as the pony cleared the barrier with the forefeet, the buzzer and/or shock were terminated. If the animal jumped over the obstacle during the CS, the trial was scored as an avoidance; if not, the trial was scored as an error. The ponies jumped first in one direction and on the next trial in the opposite direction. A pony that completed three consecutive sessions (30 trials) without receiving any shocks (0 errors) was considered to have learned and was removed from the experiment.

The data from this study were ranked according to five criteria described in Table 2. Criterion 1 (C_1) indicates long-term learning ability, or the ability to learn over an extended period of time. Criterion 2 (C_2) measures learning permanence, or resistance to extinction of learning. Criterion 3 (C_3) and criterion 4 (C_4) both reflect short-term learning. Criterion 5 (C_5) is one of the criteria used by Robustelli et al. (1963). The expression $C_5/50 \times 100$ yields the percentage of correct responses for each pony over 50 trials.

Maze learning test

The design of the maze was similar to that described and illustrated by Kratzer et al. (1977). The ponies had a choice between a right-side and a left-side escape pattern, either of which could be blocked by a movable partition. A bucket of sweet feed was placed approximately two meters from the exit of the maze as positive reinforcement for a correct choice. One maze learning trial was conducted per day before the regular morning feeding (a 17-hour fast).

For the first four trials both sides of the maze were open, allowing escape with either a right-side or a left-side choice, so that side preference could be determined. Starting on the fifth day, the partition was used to block the right-side escape pattern. When a pony correctly chose the left side first for three consecutive days, it was considered to have learned the left-side escape pattern. Thereupon the partition was moved for that pony to block the left side. The same learning criterion was applied to the right-side escape pattern. Latency (time spent in maze), initial side choice, and errors (incorrect side choices) were recorded.

Rank order in this experiment was based upon the number of days before three consecutive correct choices. Mean latency was used for ponies with equal numbers of days. The scores of the right-side and left-side preference ponies differed significantly ($P<.05$, Mann-Whitney U test) for the left-side escape pattern but not for the right-side escape pattern. Thus, only the results from the right-side escape pattern were used in establishing the rank order.

Physical measurements

The heights of all of the ponies were measured and ages were estimated by dentition. Weights were taken twice, at the beginning and end of the experimental period, and the values averaged. These variables (Table 1) and the results from all three parts of the study were then correlated, using the Spearman rank-order correlation test (Bernstein, 1964).

Results

Dominance tests

Figure 1 shows the rank order of the dominance hierarchy determined from the paired dominance (D) experiment, with the most dominant pony indicated on the left and the least dominant on the right. Triangular relationships in the dominance hierarchy are indicated by lines connecting the pairs involved. This hierarchy correlated significantly ($P<.05$) with the one obtained from the group dominance (G) test (Table 4). Paired dominance rank was also significantly correlated ($P<.01$) with the aggression (Agg) rank (Table 4). No significant correlations were found between paired dominance rank and weight, height, age, maze learning,or shock-avoidance ranks.

Avoidance learning test

Results according to five different criteria for learning are presented in Table 2. The criteria were selected to reflect different aspects of learning and to coincide with criteria used in previous shock-avoidance studies. Ponies were ranked by their performances in the shock-avoidance trials according to each of the criteria (Table 4). Ranks for all five criteria correlated significantly with each other (Table 5). The experimental ponies averaged 80 percent (range of 52-94 percent) correct responses over 50 trials.

Maze learning test

The results for this test are summarized in Table 3. Consistent side preferences were noted for all ten ponies in the maze learning (M) experiment. Seven chose the same side for all five side preference trials, while the remaining three chose the same side four out of five times. Nine of the ten ponies learned the right-side escape pattern in less than ten trials.

Significant rank correlation coefficients among the dominance rank, maze rank, the ranks for the shock-avoidance study, and age, height, and weight ranks are listed in Table 5. The maze rank correlated significantly with three of the shock-avoidance ranks (C_1, C_2,and C_5). None of the physical parameters correlated significantly with learning ability or dominance rank. No differences were found in this investigation between the performances of the ponies with cecal fistulas and those of the nonfistulated ponies.

Discussion

We draw two conclusions from this study: (1) rank in a dominance hierarchy is not correlated with, or predictive of, learning ability in

ponies, and (2) there is a significant correlation between two types of conditioned learning, avoidance and maze learning. Dominance hierarchies have been observed previously in horses and ponies, both domestic (Montgomery, 1957; Stebbins, 1973; Houpt et al., 1978) and wild (Tyler, 1972; Clutton-Brock et al., 1976; Feist and McCullough, 1976). In this study neither body size, age, nor sex determined an individual's rank in the hierarchy, but temperament was influential, as the most dominant ponies also had the highest aggression scores. The findings of other investigators on the relationship between dominance and physical parameters are varied. Montgomery (1957) stated that age, weight, and sex all affected a horse's position in the hierarchy. Age was considered by Tyler (1972) to be important in determining rank, especially at the lower end of the dominance order. Stebbins (1973) found that age and sex influenced the rank of free-ranging horses, while Feist and McCullough (1976) felt age and size to be definite factors in dominance hierarchies among stallions. According to Houpt et al. (1978), temperament was most important in determining dominance, weight had some effect on the rank order, sex seemed to have no effect, and age was only important in that mature horses were dominant over juveniles.

Paired and group dominance ranks showed highly significant correlations, suggesting that both are suitable methods for determining dominance. However, both have disadvantages. The paired dominance situation does not take into account circumstances such as the cooperation of two or more lower ranking horses in a herd against a more dominant one. In group dominance tests, the lower rank order is not always clear due to passive avoidance by the more subordinate animals, resulting in an insufficient number of interactions for accurate rank determination. In addition, group dominance ranks are based upon aggressive interactions, which are only one facet of the dominance hierarchy. However, the high correlation between the paired dominance and aggression ranks indicates that it is unlikely that an aggressive horse will be low in the dominance rank order. Since both methods of determining dominance have their drawbacks, both should be employed to get a more accurate idea of the dominance rank, although the paired dominance test would be impractical in the field.

Physical parameters and position in the social hierarchy had no relation to learning ability in maze or shock-avoidance trials. A significant correlation was found between the ponies' ranks in maze learning and shock avoidance learning ability. This is particularly interesting, since one type of learning involves conditioning to avoid a negative reinforcement (electrical shock), while the other uses a positive reinforcement (highly palatable food) to condition the animal. In contrast to this study, maze and shock-avoidance learning were not correlated in swine (Hammell et al., 1975) or rats (Robustelli, McGough and Bovet, 1963). This may be due to either a species difference or a difference in experimental procedure. For example, Hammell et al. (1975) used a water maze with return to the litter as the positive reinforcement for suckling piglets. Physical attributes and swimming ability may have been as important as learning ability in the young pigs. Also, mazes used by Hammell et al. (1975) and Robustelli et al. (1963) were more complicated (three and eight point choices, respectively) than the one choice-point maze used in this study.

The correlations between maze rank and the ranks for C_1 and C_2 of the shock-avoidance study, as well as the highly significant correlation between C_1 and C_2 (Table 5), suggest that long-term learning and learning permanence are related. The rank order for C_5 also correlated significantly

with maze rank (Table 5). This indicates that ponies which made fewer errors in the shock-avoidance experiment also made fewer errors in the maze learning test. Thus, for ponies, better learners in a classical conditioning situation tend to learn more quickly in an operant conditioning situation as well.

Although learning ability and dominance hierarchy did not correlate significantly in this study, both aspects of behavior are important for survival. Learning ability is an individual phenomenon based upon each animal's genetic background and experience, while dominance hierarchies are relative to the groups in which they are formed. The position of an animal in the hierarchy will vary depending upon the group, since the members of groups differ in tendencies to be dominant or subordinate. A more accurate indication of the relationship between learning ability and dominance hierarchies might be achieved by conducting a study similar to this one on herds of feral horses where the dominance hierarchies have been established for a long period of time and the genetic backgrounds and experiences of herd members are more similar than those of the ponies used in this experiment.

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TABLE I. PHYSICAL MEASUREMENTS OF THE PONIES USED IN THE DOMINANCE AND LEARNING EXPERIMENTS

Pony number	Sex	Age (A) (years)	Height (H) (cm)	Weight (W) (kg)
26	F[a]	7.0	115.2	186.1
416	M[b]	2.5	106.2	135.0
407	F	9.0	102.4	145.8
411	F	5.0	107.5	154.8
11	F	13.0	103.7	162.2
20	G[c]	9.0	106.2	158.4
9	F	3.0	109.4	135.0
282	M	2.0	102.4	98.8
16	F	7.0	102.4	144.0
27	G	16.0	110.7	191.2

[a] Female

[b] Male

[c] Gelding (male castrate)

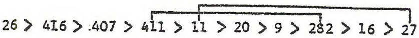

Figure 1. Rank order of the dominance hierarchy determined for a group of 10 ponies in a paired dominance test.

TABLE 2. RESULTS OF THE SHOCK-AVOIDANCE STUDY FOR
FIVE LEARNING CRITERIA

Pony number	Criterion 1 (C_1)[a]	Criterion 2 (C_2)[b]	Criterion 3 (C_3)[c]	Criterion 4 (C_4)[d]	Criterion 5 (C_5)[e]
26	6	8	6	11	44
416	26	26	20	25	26
407	4	6	2	2	46
411	1	3	1	1	47
11	17	17	3	3	38
20	12	13	2	3	42
9	10	10	4	5	40
282	8	16	3	5	40
16	21	37	21	27	28
27	2	3	2	3	47
Mean	10.7	13.9	6.4	8.5	39.8
Median	9	11.5	3	4	41

[a] Total number of shocks before a session of 10 avoidances

[b] Total number of shocks before three consecutive sessions of 10 avoidances or total number of shocks received in the experiment

[c] Total number of shocks before three consecutive avoidances

[d] Total number of trials before three consecutive avoidances

[e] Total number of conditioned responses (avoidances) over a five-day period

TABLE 3. SIDE PREFERENCE AND PERFORMANCE IN THE MAZE LEARNING EXPERIMENT

Pony number	Side preference	Number of days before three consecutive correct choices		Mean time through maze (sec)	
		Right	Left	Right	Left
26	right	2	2	15.9	12.2
416	right	10	3	59.4	24.4
407	right	2	4	10.8	14.2
411	right	3	2	12.3	13.6
11	left	4	0	17.0	8.6
20	right	3	3	13.6	9.4
9	right	2	3	8.8	9.0
282	left	6	5	11.8	11.8
16	right	9	6	13.1	5.8
27	left	2	0	10.4	7.0
Mean		4.3	2.8	17.3	11.6
Median		3	3	13.4	10.6

TABLE 4. RANK ORDERS FOR THE RESULTS OF THE DOMINANCE TESTS, THE MAZE LEARNING EXPERIMENT, AND THE SHOCK-AVOIDANCE STUDY

Pony number	Paired dominance rank (D)	Group dominance rank (G)	Aggression rank (Agg)	Maze rank (M)	Shock-avoidance rank				
					C_1	C_2	C_3	C_4	C_5
26	1	2	1	4	4	4	8	8	4
416	2	1	2	10	10	9	9	9	10
407	3	3	3	3	3	3	3	2	3
411	4	4	5	5	1	1.5	1	1	1.5
11	5	10	4	7	8	8	5.5	4	8
20	6	5	7	6	7	6	3	4	5
9	7	7	8	1	6	5	7	6.5	6.5
282	8	8	10	8	5	7	5.5	6.5	6.5
16	9	6	6	9	9	10	10	10	9
27	10	9	9	2	2	1.5	3	4	1.5

TABLE 5. SIGNIFICANT RANK CORRELATIONS FOR THE RESULTS OF THE DOMINANCE, MAZE LEARNING, AND SHOCK-AVOIDANCE STUDIES AND THE VARIABLES FROM TABLE 1

Correlation	r value	Correlation	r value
D & G	.77*	C_1 & C_5	.96***
D & Agg	.89***	C_2 & C_3	.76*
M & C_1	.69*	C_2 & C_4	.72*
M & C_2	.80**	C_2 & C_5	.97***
M & C_5	.72*	C_3 & C_4	.96***
C_1 & C_2	.95***	C_3 & C_5	.81**
C_1 & C_3	.74*	C_4 & C_5	.74*
C_1 & C_4	.69*		

*$P < .05$

**$P < .01$

***$P < .001$

Band Organization and Stability in Red Desert Feral Horses

Richard Miller
Department of Zoology, University of Wyoming, Laramie

Abstract

Band structure, social organization, behavior, movements, and habitat use of feral horses (Equus caballus) in Wyoming's Red Desert were studied from 1976 to 1979. Three types of horse bands were described: bachelor male groups, single male bands, and multiple male bands. Average band size declined from 8.4 horses in 1977 to 7.1 horses in 1978 and to 6.9 in 1979. The average size of multiple male bands ranged from 9.3 to 9.6 horses during the study, while single male bands were significantly smaller, averaging 5.8 to 6.8 horses over the study. The adult membership of multiple male bands changed less frequently than did adult membership of single male bands. In 1979 rates of change in membership increased greatly, possibly as a result of a severe winter in 1978/79. The proportion of multiple male bands declined from 45 to 23% of the bands between 1977 and 1979. Dominance rank of males was often reflected in the band's order of travel. Adult males both led and trailed bands more often than did females. Changes in band organization and stability appear to be a response to changes in the horses' environment.

Introduction

A variety of social organizations have been described for both feral burros and feral horses in North America. Male feral burros in the Chemehuevi Mountains of California rarely defended territories, and estrous females attracted large groups of males (Woodward, 1979). Male territoriality and some breeding on the territories have been reported in feral burros of Death Valley (Moehlman, 1974, 1979). Single adult male and multiple adult male harem groups of feral asses were territorial on Ossabaw Island (McCort, 1979). All three of these authors attributed the differences between populations to environmental factors. Feral horses in the Grand Canyon (Berger, 1977) and in the Wassuk Mountains of Nevada (Pellegrini, 1971) are found in bands with a single adult male; these bands rarely associate with one another. Bands of feral horses with both single and multiple adult males and overlapping home ranges have been reported in Stone Cabin Valley, Nevada (Green and Green, 1977).

The purposes of this paper are: 1) to describe the social organization of feral horses in Wyoming's Red Desert , 2) to describe changes in that social organization and 3) to suggest possible environmental causes for those changes in social organization.

Methods

The Red Desert study lies in Sweetwater County of southwestern Wyoming. Information was gathered primarily on eight townships (737 sq. km) along the Kilpecker Dune Field (Ranges 98, 99, 100, and 101 west, Townships 23 and 24 north). The Bureau of Land Management estimated the feral horse population on the Rock Springs District (56,400 sq. km), which contains the study area, as 5500 animals in 1976, 6263 in 1977, and 5459 in 1978 (Bureau of Land Management, 1979). From June 1976 to November

1979 I spent over 1000 hours observing horses on the study area. I made observations using a 20-power spotting scope and 8-power binoculars and recorded them directly into notebooks.

A band is defined as a group of horses which normally move together, containing at least one adult male and usually several adult females with their offspring (Miller and Denniston, 1979). A bachelor group consists of males moving as a unit, without any attached females. The term bachelor group was used rather than bachelor band to indicate the instability of a bachelor group relative to a band. Bands and individual horses were identified using a photo file and a separate card file, keyed both on color combinations and on readily identifiable individual horses. By the end of the study 68 bands and eight individuals were included in the photo file, and 159 bands were described in the card file. Each band and some bachelor males were assigned letter designations, beginning with A and ending with GO, which are used in this paper. Horses up to two years old were aged by height and tail length. Any horse over two years old was classed as an adult. We considered horses whose tails just reached their hocks to be yearlings. This corresponded well with known aged yearlings until spring 1979, when tail lengths of some known aged yearlings were shorter. Shorter tails may have been a result of poor growth in the relatively severe winter of 1978/79.

When a known band was sighted, its location, activity, and composition were recorded. If it was a band which I intended to study that day, the band became the focus for recording behavior. A scanning method of observation was used, because the level of activity was rarely high enough to prevent me from observing all behavior of interest in a band. Occasionally more than one band could be scanned simultaneously, as at a water hole. One or two horses became the focus of observations during aggressive encounters or breeding. An effort was made to regularly locate and identify as many of the bands as possible. My field time was concentrated during the summer, but some observations were made in every month of the study.

Data from all bands identified in a year were used to calculate mean band size for all bands. I used only those bands for which the sex of all adults was known and which were located often during a year in calculations involving best known bands, multiple male bands, or single male bands. Band stability, or fidelity, was measured as the number of adult horses changing bands in a year per 100 horses. I excluded foals, yearlings, and two-year-old horses from these stability calculations, because young horses normally move between bands and are not a good measure of band stability. Bachelor male groups were also excluded from the calculations because of their frequent changes in membership. Data from 1976 were excluded, because too few bands were described and regularly seen to give an adequate sample. Mean band sizes were compared using a t-test for unequal sample sizes; the other comparisons were made using Chi-square contingency tables (Sokal and Sohlf, 1969).

Results and Discussion

Three basic types of bands exist in the Red Desert: bachelor male groups (one to 16 horses), multiple male bands (mixed sex bands of three to 17 horses, including two to five adult males), and single male bands (mixed sex bands of two to 21 horses, including one adult male).

Bachelor groups were generally unstable in composition. Often a bachelor male was associated with two or more different bachelor groups on

the same day. However, I always observed one pair of bachelors together over 2.5 years, and another pair was always observed together for over 22 months. Similar long-lasting associations between bachelor males have been reported in plains zebra (*Equus quagga*) (Klingel, 1969). In the spring of 1979, when the multiple male bandsFW and M broke up, males from these bands formed bachelor pairs. Each newly formed bachelor pair was seen together every time they were located for three months thereafter. The M males were father and son. One FW male was a bachelor in 1977, and was a member of Band FE during the summer of 1978. He then left Band FE and formed Band FW with one female and another male during the winter of 1978/1979 or early spring 1979. The two males in FW had not been seen together regularly before 1979.

Salter (1978), Hall and Kirkpatrick (1975) and Feist and McCullough (1976) found that dominance hierarchies exist in bachelor groups. Because of the small amount of time I spent observing bachelor groups and the shifting membership of those groups, such a hierarchy was not documented in this study. However, it was apparent that bachelors both alone and in groups were subordinate to males in bands (Miller and Denniston, 1979).

Multiple male bands have previously been reported on Assateague Island (Keiper, 1976); in the Pryor Mountains (Hall, 1972); in Alberta (Salter, 1978) and on Sable Island (Welsh, 1975). I believe that multiple male bands require separate consideration, because of the differences in multiple male and single male bands with respect to male breeding behavior, dominance structure (Miller, in prep. a), average band size, and band stability. From 23% to 45% of the bands described each year during this study were multiple male bands. The percent of multiple male bands declined significantly between 1977 and 1979. Dominance in multiple male bands and interband dominance is described elsewhere (Miller, in prep. a; Miller and Denniston, 1979).

Single male bands are basic to the social organization described by Klingel (1974) for non-territorial equids. This type of band has been described in previous research on feral horses (Berger, 1977; Feist and McCullough,1976; Green and Green, 1977; Hall and Kirkpatrick, 1975; Pellegrini, 1971; Salter, 1978; and Welsh, 1975). Although the average band size of single male bands was significantly less in each year than that for multiple male bands (Table 1), some of the largest bands were single male bands. A single exceptionally aggressive male may be able to maintain as large a band as several less aggressive males. The position of three single male bands at the top of the interband dominance hierarchy reported by Miller and Denniston (1979) also suggests high levels of aggression in the males controlling large single male bands.

Average band size for all bands was 6.9 to 8.4 horses between 1977 and 1979 (Table 1). This is larger than band sizes reported for feral horses in Arizona (Berger, 1977), in the Pryor Mountains (Hall, 1972; Feist and McCullough, 1975), and in Nevada (Green and Green, 1977; Pellegrini, 1971). However, Salter (1978) has reported band sizes for feral horses in Alberta similar to the Red Desert average, and Keiper (1976) reported a band size for feral ponies larger than the Red Desert average.

Average band size for all bands declined significantly (p=0.05) between 1977 and 1979, despite the relatively constant average size of both multiple male and single male bands (Table 1). These declines may be accounted for by the decrease in the proportion of multiple male bands over the same period. Because multiple male bands were consistently larger than single male bands (Table 1), a lower proportion of multiple male bands would also lower the average band size.

Both multiple male and single male bands were normally stable in membership, averaging 0.75 adult changes/band/year. For many of the bands, all the adult horses in the band in 1977 were still present in 1979. The average number of changes per band was raised by data from a few bands, such as AE, which decreased from 20 horses in 1978 to eight horses in 1979. Plains zebra groups are similarly very stable, with 95% of the females in the same groups after two years (Klingel, 1969). Feist and McCullough (1975) reported ten adults changing bands in six months, or 11.6 changes/100 horses/year, which is within the range reported here. Welsh (1975) recorded 356 changes within 2.5 years in a population of approximately 250 horses, but he included both adult and young horses in his analysis.

The decrease in the proportion of multiple male bands in 1979 was accompanied by a decrease in the stability of the best known bands (Table 2). The majority of horses changing bands in 1979 did so during the winter or early spring. Thirty-five of the 60 band changes in 1979 occurred before the end of May, as compared to 1978, when only five of 26 band changes took place by the end of May. The number of winter and spring band changes suggests that the decrease in band stability may have been caused by stress during the severe winter weather of November 1978 through January 1979 (Table 3). Keiper (1976) has reported feral pony bands breaking into smaller units during late fall and winter, but he did not mention any relation between this behavior and weather.

Multiple male bands were consistently more stable in membership than the single male bands (Table 2). The greater stability in multiple male bands may be a result of the aggressive behavior of subordinate males protecting and maintaining the band (Miller, in prep. a). Welsh (1975) suggested the band maintenance activities of subordinate males may make larger band sizes possible in multiple male bands. Although some subordinate males breed, the greater stability and larger average size of multiple male bands may amount to an increase in the availability of breeding females to the dominant male, accounting for his tolerance of subordinate males. Welsh (1975) has shown that foaling rates and foal survival were lower in small bands and in unstable bands on Sable Island. If Welsh's data can be applied to the Red Desert horses, the gains in numbers of offspring to the dominant male may be greater than gains in numbers of females.

Males may alter or form bands in at least six ways: 1) a bachelor male may gain control of one or more females which are separated from their band; 2) a bachelor male may attach himself to an established band; 3) a bachelor male may acquire an intact band; 4) a male accompanied by a female may leave a multiple male band; 5) a male from a multiple male band may acquire a female or females from another band and leave his original band; or 6) a male born in a single male band may remain in that band as an adult (Denniston, in press). Examples of alternatives 1, 2, 4, 5 and 6 were observed in this study, and Keiper (1976) and Klingel (1969) report examples of alternative 3.

I observed only 27 alterations or attempted alterations in band structure as outlined in the above six alternatives. The remainder of the 112 adults changing bands did not affect band structure except to change the number of males within a multiple male band or females within a band.

The most common mechanism of band formation was for a bachelor male to acquire a female or females. I observed nine successful acquisitions of mares and four unsuccessful attempts by bachelor stallions. Most of the unsuccessful attempts failed due to the efforts of the females to return to their original bands. Seventeen mares were able to return to their original bands after being controlled by a bachelor or a male from

another band. Mares still attempted to return to their original bands as long as two days after leaving. Female ponies and zebra sometimes leave and then return to their original bands after absences of several days (Klingel, 1969; Keiper, 1976).

Ten bachelor males attempted to join existing bands, and in four instances they succeeded in remaining with the new band for more than one month. Three of them were still with the new bands when the study ended, after periods of up to five months. Some bands were followed by as many as three bachelors at a time. "Tag alongs", such as these, are also found on Sable Island (Welsh, 1975) and in the Pryor Mountains (Hall and Kirkpatrick, 1975). A "tag-along" may be able to increase his probability of breeding and may become the subordinate male in a multiple male band.

Two stallions took over intact bands after the original males died on Assateague Island (Keiper, 1976). In at least two of five reported cases of plains zebra males taking over intact family groups, the original stallions had not died (Klingel, 1969). While this may occur in the Red Desert, I did not observe it.

Only one observation was made of a male from a multiple male band permanently leaving his original band with a mare from the band. Green and Green (1976) have reported twice observing two males splitting a band between them.

Three Red Desert stallions left multiple male bands after acquiring mares from other bands. When a subordinate male attempted to bring a new mare into his original band, the dominant male always prevented it. The dominant male's aggression was directed at the new mares except when the subordinate male attempted to come between the dominant stallion and the new mare. This aggression may be the mechanism by which some subordinate males leave multiple male bands. In four other instances males chased away strange females which wandered into their bands. This is in contrast to the Assateague Island ponies, where mares frequently left their bands to join other bands for a few days before returning to their original bands (Keiper, 1976).

I know of only one stallion which matured and bred in its original band. That stallion was part of a multiple male band (Band L) which remained at approximately 12 horses throughout the study. This male became dominant for a time and bred when he was four years old (Miller, in prep. a). I do not consider this necessarily a rare occurrence, because by the end of the study the only known age horses which might have been breeding were yearlings in 1976, and few yearlings were described in 1976.

It is remarkable that more alterations and band formations did not take place, considering the opportunities. On 57 occasions members of bands became separated, and despite the fact that bachelor groups and other bands were usually present, no attempts were made by any males to gain females. As a comparison 112 changes in the adult membership of bands were recorded over the same period. Most of these separations occurred at water, when part of a band left a waterhole while the remainder continued to drink. The animals remaining at water were usually mares or young horses. Separations also occurred when the stallion of a single male band chased a female from another band, leaving his mares. In these instances the bands were often reunited through the efforts of the females rather than the males. The separated horses were generally ignored by bachelor male groups and other bands which happened to be in the same area.

The order of travel within the bands was recorded most often when

bands were moving to or from waterholes, because at these times a band normally traveled in single file. Then bands often moved rapidly and in groups making recording the entire order of travel for any one band difficult. The result was that leading horses were recorded more often than trailing horses.

Males led slightly more often and trailed much more often than females (Table 4). Both yearlings and foals occasionally led or trailed. Leading by foals and yearlings was most frequent when they ran ahead in play or when their dam was the second horse in the order (Lee Boyd, Department of Zoology and Physiology, University of Wyoming, pers. comm.). A lead female most often initiated and led movements in the Pryor Mountains (Hall and Kirkpatrick, 1975). Stallions in the Grand Canyon more often led into water, while females most often led away from water (Berger, 1977). In the Red Desert, when approaching another band a male would often move to the front of his band. If two bands were traveling close together in the same direction on a trail, then a male in the lead band was likely to be last in his band, while a male would usually lead the second band. At other times males would often place themselves between their band and other bands; this may be part of the male's role in protecting the band from other males.

The order of travel in some bands was very consistent. If the adults present in Bands H and Y from 1977 through 1979 are considered, the order of travel for those adults was consistent in 63% (n = 43) and 85% (n = 33) of the observations, respectively. The order of travel often reflected the dominance rank of males within some bands with dominant male in front of second ranked male and so on (males of Bands H, A, FJ, and EG, Table 5). In contrast, Wells and Goldschmidt-Rothschild (1979) found no direct relationship between traveling order and rank or age in Camargue horses. Bachelor males had attached themselves to Bands FJ and EG, and male hierarchies in both bands were linear and well defined (Miller, in prep. a). This may have contributed to the consistency of rank order movement in Bands FJ and EG. In some bands the lead or the trailing horse or both were very consistent in the order of travel. One male in Band L trailed 97% of the time, if a bachelor male which followed the band from 13 May 1979 to between 28 and 30 May 1979 is not included in the analysis. During this time the newly attached male trailed on five of five occasions.

Unlike Feist and McCullough (1976), I have not included herding by males in initiation of movement, because it is primarily an aggressive behavior and will be discussed in another paper (Miller, in prep. a). I recorded initiation of movement only if one horse clearly made the first move in the direction subsequently taken by the entire band. Adult females initiated more than half of the movements, while adult males initiated just over a third of the movements (Table 4).

A herd of feral horses is defined as a structured social unit made up of bands following similar movement patterns within a common home range (Miller, in prep. b). It is necessary to consider that the band structure and behavior described exist within the structure of a larger social unit. The high band stability may be a result of the existence of a herd, and the changes I have reported may in fact be a result of a change in herd, not band, structure. The existence of herds could account for some of the discrepancy between the average band size for all bands and that for best known bands (Table 1). The best known bands are largely all from one herd, and if average band size differs between herds, then the discrepancy may be explained by herd differences.

A herd can be distinguished by seasonal movements and long term association between bands; however, the bands of a herd cannot be distinguished by short-term association between bands. Often feeding groups of 50 to 150 horses composed of bands from one or more herds were within a one square mile area, and larger concentrations are sometimes found at waterholes (Miller and Denniston, 1979). Feeding groups sometimes travel to waterholes as loose units. These groups are not permanent associations and may be caused by a behavioral tendency to aggregate or by selective feeding on patches of relatively high quality forage. A herd cannot be distinguished in these feeding groups.

It is unusual to find a band that is not near other bands and even more unusual to find completely solitary horses. Completely solitary horses (those which were far enough from other horses to be counted as a lone horse) were very rare, averaging only 0.25% of the total horses counted on 16 aerial counts, with a range between 0.0% and 0.73%. The number of horses which act and move as individuals rather than as members of a group or band was not accurately reflected in aerial counts of solitary animals, because these horses were most often so closely associated with bands or bachelor groups as to be counted in with another band or group. However, this low figure indicates that it was very rare for any horse to be completely solitary and away from other horses. All but one of the solitary horses recorded during ground observations were males.

A number of authors have theorized about the relationship between a species' environment and its social organization (Crook, 1970; Eisenberg, et al., 1972; Geist, 1974; Jarman, 1974; Crook, et al., 1976; Clutton-Brook and Harvey, 1977, 1978). Also, several authors report or suggest that a species' social organization can change in response to environmental conditions within one generation (Eisenberg, et al., 1972; Altmann, 1974; Geist, 1974). Jarman (1974) recognized seasonal and regional variation in group size within a species and attributes the variation to changes in the amount and dispersion of food items. Sinclair (1977) found that fragmentation of preferred habitat caused herds of African buffalo to split into smaller units. Horse bands in the Red Desert may have been similarly affected during the winter of 1978/79, when deep and persistent snow limited the forage available to the horses. Also, water availability increased after the summer of 1977 with the creation of two new waterholes within 4.5 km of a heavily used waterhole. That area was used during and after the period when most foaling occurred. Large bands were dominant over smaller bands competing for access to the waterhole (Miller and Denniston, 1979), and creation of two new water sources nearby may have decreased competition for water and reduced the pressure for large band size.

The existence of multiple male bands in primates has been explained as a reaction to predator pressure (Crook, 1970; Crook et al., 1976; Clutton-Brook and Harvey, 1977) and as a response to habitat type (Bourliere and Hadley, 1970). Since no evidence of predation was observed during this study, multiple male bands may prove to be an adaptation to resource distribution in the Red Desert. Some authors suggest that large bands are adaptations to clumped food resources (Altmann, 1974; Clutton-Brook and Harvey, 1977) and that band size and social organization are closely linked (Alexander, 1974; Jarman, 1974). Food resources in the Red Desert are patchy in distribution in spring when green-up occurs first along water courses, in fall when forage in moist areas remains green longer, and in winter when food availability can be determined by snow distribution.

Variation in the size of family groups in plains zebra correlates with rainfall (Klingel, 1969). In plains zebra the number of adult females in family groups did not vary as much as total group size between areas, and social structure did not vary with band size. The range in the number of females per band is similar for plains zebra, 2.2 to 2.8 females per band (Klingel, 1969), and for feral horses in the Red Desert, 2.0 to 2.9 females per band (Lee Boyd, Department of Zoology and Physiology, University of Wyoming, pers. comm.). However, in the Red Desert the variation is between band types, with multiple male bands having more females, and not between locations. Also there is a relationship between band size and band organization in the Red Desert.

Data suggest that the dominant male in a large multiple male band may have greater access to adult females. Welsh (1975) suggests a greater reproductive success over time in large bands. Thus, multiple male bands may be formed whenever environmental conditions permit formation of large bands of feral horses.

Previous authors have suggested the conditions favorable for herd formation. If several essential resources have a very restricted distribution, Altmann (1974) predicts home range overlap will be high. This may explain the common home ranges of bands in a herd, since water, winter forage, cover, and at certain times of the year green forage have a restricted distribution in the Red Desert. Crook, et al. (1976) similarly suggested that where large home ranges are necessary, patchy resources may result in common use of a range by several mating groups which together form large herds.

The data demonstrate that feral horse social organization can change measurably in three years and that the social organization of feral horses in the Red Desert may fit some of the current theories on social organization and environment. The variability of feral horse social organization both between locations and through time makes these animals good subjects for future testing of social organization theory.

Summary

1. There were three types of feral horse bands in the Red Desert: bachelor male groups, multiple male bands, and single male bands.
2. Bachelor groups were normally unstable in composition, although some pairs of males were observed together for more than two years.
3. The proportion of multiple male bands declined from 45% to 23% of the bands between 1977 and 1979.
4. Average band size changed from 8.4 horses in 1977 to 6.9 in 1979, while the average size for multiple male and single male bands considered separately remained stable.
5. Multiple male bands were significantly larger than single male bands in all years.
6. The decline in the proportion of multiple male bands in 1979 was accompanied by a decline in band stability.
7. Multiple male bands were consistently more stable than single male bands.
8. The most common means of forming a band was for a bachelor male to acquire a female from an established band.
9. The most common alteration in band structure was for a bachelor male to attach himself to an established band.
10. Adult males led most often, but only slightly more often than adult

females. Adult males trailed their bands much more often than did adult females.

11. The order of travel in a band often reflected the dominance rank of males in that band, the dominant male being the first male in the order. The order of travel of some bands was very consistent.
12. Adult females initiated most band movements.
13. The band structure described in this paper existed within the framework of a herd made up of bands. The herd structure may contribute to some of the changes seen in band structure.
14. The changes in band structure and stability may have been in response to changes in the availability of resources to the feral horses.

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Table 1. Average size of feral horse bands in Wyoming's Red Desert, 1977-1979.

Average Band Size For	1977	1978	1979
All Bands	8.4	7.1	6.9
(sample size)	(77)	(81)	(100)
significance	a***		a***
Best Known Bands	7.4	7.6	6.9
(sample size)	(32)	(44)	(52)
Significance			
Multiple Male Bands	9.4	9.6	9.3
(sample size)	(14)	(18)	(12)
significance	b*	c***	d***
Single Male Bands	5.8	6.8	6.2
(sample size)	(18)	(26)	(40)
significance	b*	c***	d***

Sample size is in number of bands. Any two statistics which are followed by the same letter are significantly different at the level indicated by the asterisks: $*\alpha = 0.2$, $***\alpha = 0.05$. All other comparisons are nonsignificant at the $\alpha = 0.2$ level. Best Known Bands are those bands which were located often and in which the sex of all adults was known. Data for multiple male and single male bands are subsets of the data for best known bands.

Table 2. The number of adult feral horses changing band membership per 100 band members, 1977-1979.

Rates of Change for	1977	1978	1979
All Bands	7.0	7.4	15.8
(sample size)	(370)	(351)	(380)
significance	a***	b***	a***b***
Multiple Male Bands	4.5	4.1	11.7
(sample size)	(132)	(169)	(111)
significance	c***d**	e***f**	d**f**g*
Single Male Bands	15.0	11.4	17.0
(sample size)	(105)	(166)	(247)
significance	c***	e***h*	g*h*

Sample size is in number of horses. Any two statistics which are followed by the same letter are significantly different at the level indicated by the asterisks: *$\alpha = 0.2$, **$\alpha = 0.1$, ***$\alpha = 0.05$. Best known bands are those bands for which the sex of all adults was known and which were located often. Data for multiple male and single male bands are subsets of the data for best known bands.

Table 3. Departures of average monthly temperature and total monthly precipitation from winter normals at the Rock Springs, Wyoming, FAA recording station (NOAA, 1976, 1977, 1978, 1979).

Winter	November		December		January		February		March	
	Temp. (°F)	Precip. (in.)	Temp. (°F)	Precip. (in.)	Temp. (°F)	Precip. (in.)	Temp. (°F)	Precip. (in.)	Temp. (°F)	Precip. (in.)
1976/77	+ 2.4	- .53	+ 3.9	+ .36	+ 3.3	- .19	+ 7.4	- .52	- 1.1	+ 1.27
1977/78	+ 1.3	+ .19	+ 5.0	- .07	+ 4.9	+ 1.08	+ 4.1	+ .69	+ 8-7	+ .30
1978/79	- 6.1	+ 1.06	-10.0	+ .07	-12.4	+ .93	+ 0.9	- .22	+ 3.6	- .17

Table 4. Feral horse band leadership.

	Percent of Observations		
	Leading (781)	Trailing (423)	Initiating movement (63)
Adult Males	50	73	38
Adult Females	48	19	59
Yearlings	2	5	3
Foals	1	4	0

Sample size in number of observations is shown in the parentheses.

Table 5. Order of travel for selected bands of feral horses in the Red Desert.

	Horse Most Often Leading				Horse Most Often Trailing				Males in Rank Order, with Dominant Male as First Male		
Band	% of obser.	sex	rank	sample size	% of obser.	sex	rank	sample size	% of obser.	no. of males	sample size
A	—	—	—	—	—	—	—	—	89	2	27
H	71	M	1 of 2	55	74	M	2 of 2	43	81	2	43
L	55	M	?	118	91	M	?	91	male ranks varied		
AC	—	—	—	—	—	—	—	—	75	2	24
AP	—	—	—	—	—	—	—	—	60	3	20
EG	52	M	1 of 3	29	96	M	3 of 3	27	96	3	27
FJ	56	F	?	22	90	M	2 of 2	22	95	2	21

Biogeography and Habitat-Use Behavior of Feral Horses in Western and Northern Canada

R. E. Salter
Department of Animal Science, University of Alberta, Edmonton, Canada

Abstract

Current estimates of feral horse populations in western and northern sub-arctic Canada indicate that ~900 animals occur in Alberta, ~200 are present in British Columbia, and an additional 200-300 are found in Yukon Territory. These animals occupy areas characterized by coniferous forest cover and relatively cold climate. Studies in western Alberta showed that under favorable conditions the foal and yearling cohorts may together constitute 35% of the population, indicating a potential for rapid population growth; however, starvation and high levels of predation during severe winters are thought to be limiting factors. The Alberta studies are used to illustrate various aspects of habitat-use behavior (home range size, habitat selection, snow relationships, use of shelter, food habits, drinking, use of mineral licks); comparative aspects of habitat-use by feral horses in other areas of the northern coniferous forest in Canada are discussed. Reported land-use conflicts involving feral horses include competition for forage between horses and cattle, competition between horses and wild ungulates, and grazing and trampling damage on spring ranges.

Introduction

Although the present North American population of feral horses is concentrated in desert and semi-desert areas of the western United States, numbers also occur in western and sub-arctic northern Canada. These horses are the descendants of strays or escapees from resident Indian tribes (who had acquired horses by the mid-1700's), and from mining, ranching, and forestry activities that accompanied settlement during the last century. The most recent additions have been from unmanaged Indian herds, and from stock maintained by guides and outfitters in remote areas (Salter and Hudson, 1978a).

It can be inferred from the known distribution of these animals (McKnight, 1959, 1964) that they are found in areas characterized by predominantly coniferous forest cover and relatively cold climate, but detailed ecological studies have only recently been carried out (Storrar et al., 1977; Salter, 1978a). The purpose of this paper is to summarize available information on distribution, numbers, and habitat relationships (use of vegetation types, use of space, food habits, land-use conflicts) of feral horses in western and northern Canada.

Distribution and Numbers

According to questionnaire surveys and interviews of Forest Service and wildlife management personnel conducted during 1975-79, there are now in the order of 1400 feral horses in British Columbia, Alberta, and the Yukon Territory. (This is a gross estimate only; it is based on the 'best guess' of field personnel, but most regional population estimates are not based on any standard survey methodology.) Fewer than 200 feral horses were reported in British Columbia, but the number there may be much higher as no information is available from a large area in the northwestern part of the province. Nine hundred feral horses were reported in Alberta, and an additional 200-300 in Yukon Territory. Substantial numbers of free-ranging Indian and outfitter horses were reported for both provinces--600 and 200, respectively, in British Columbia, and about 700 and 100, respectively, in Alberta. Eight hundred free-ranging outfitter horses were reported to be present in the Yukon. Herds in these categories are often difficult to distinguish from feral stock, and in some areas may continue to contribute to feral horse numbers.

Known numbers of truly feral (unowned) horses are presently concentrated along the eastern slope of the Rocky Mountains, where at least 700 horses are present between the Bow and North Saskatchewan Rivers (Figure 1). This foothill area is characterized by forest cover of lodgepole pine (Pinus contorta), with smaller stands of white spruce (Picea glauca), black spruce (P. mariana), alpine fir (Abies lasiocarpa), aspen poplar (Populus tremuloides), balsam poplar (P. balsamifera), and mixed woods. Meadow and shrub vegetation types cover ~20% of the area. Drainage is through numerous permanent streams. Climate of the area is classified as cool and subhumid (Table 1); during most winters, much of the snowfall is periodically removed by warm west winds.

An additional 100 or more animals occur in the Cariboo-Chilcotin area of British Columbia. Forest cover in this flat to gently rolling region is dominated by lodgepole pine; small mesic meadows surrounded by aspen poplar are characteristic. Climate is characterized by warm, dry summers and cold winters.

The main concentration of feral horses in Yukon Territory is in the Nordenskiold River area, a region characterized by extensive forest cover dominated by white spruce, with smaller areas of lodgepole pine forest and black spruce muskeg. Open habitats include burns, south-facing grassy slopes, and sedge fens. The area has short, cool summers and cold winters; daily temperatures average above 0°C only during May-September.

Population Trends

Areas of concentration have remained about the same over the last two decades or more, at least in Alberta and British Columbia (McKnight, 1959, 1964), although total numbers of feral horses may have declined somewhat. McKnight reported between 1000 and 2000 feral horses in the southern half of British Columbia and from 1500-2000 animals in Alberta,

but it should be recognized that these are very rough estimates and the figures may have included some Indian and guide horses. McKnight did not report population estimates for the Yukon Territory.

Current trends in regional population levels appear to be due at least in part to level of management. In British Columbia, where populations are generally considered to be stable or decreasing, there has been a concerted effort to control numbers of free-ranging horses through roundups and shooting since the 1920's, and this effort continues to date (Storrar et al.,1977; Salter and Hudson,1978a). Numbers of free-ranging horses in Alberta were controlled through extensive roundups until the early 1970's; controls on feral horse populations have not been initiated since that time, and numbers are considered to be increasing in some foothill areas (Salter and Hudson, 1978a). Government controls on feral horse numbers have apparently never been instituted in the Yukon; it is not known whether populations there are presently increasing or decreasing.

Feral horse populations in western and northern Canada likely undergo natural fluctuations, although detailed studies of population dynamics have not been conducted. A study conducted in western Alberta (Salter, 1978a) showed that during mild winters, and in the absence of significant predation, there may be nearly complete over-winter survival of the foal cohort. During a year of intensive study foals and yearlings comprised 18% and 17%, respectively, of the population; this suggests a potential for rapid population growth. However, local residents and management personnel reported that abortions and high mortality rates due to starvation occur during winters with deep snow and abnormally cold temperatures, thus limiting local populations. Predation by cougars and wolves is reportedly also a source of mortality, particularly during severe winters.

Habitat-Use

Quantitative studies of habitat-use by feral horses have been conducted in western Alberta (Salter, 1978a) and in the Chilcotin region of British Columbia (Storrar et al., 1977). Limited qualitative information on habitat-use was obtained during questionnaire surveys and interviews referred to above.

Use of Space

During the study conducted in western Alberta the horse population was organized year-round into two basic herd types--harem groups and bachelor stallion groups. Herds occupied overlapping home ranges of less than 15 km^2; all home ranges included both non-forested (meadow and shrub) and forested habitat.

Habitat Selection

Pellet group counts, dietary data, and sightings of horses indicated that feral horses in western Alberta made use of virtually all available habitats. Pellet groups occurred on 85% of plots examined during summer (Table 2); they did not occur in any one habitat more frequently than

expected but on the basis of total counts certain meadow and shrub types (dwarf birch thicket, mixed shrub meadow, dwarf birch meadow) and adjacent forest types (black spruce woods) appeared to be most heavily utilized on a year-long basis. Poplar woods were heavily utilized during winter; use of this limited habitat appeared to be related to its proximity to concurrently used south-facing grassy slopes, and possibly to reduced snow depth due to southerly exposure. However, only habitats that were limited in areal extent or that had sparse forage growth were clearly under-utilized during winter. Habitat occupancy during spring was related to stage of forage growth; previously grazed meadows and disturbed areas were the first to green up and were heavily used for feeding. Horses also fed under forest cover during spring. The pattern of use of both forested and meadow habitats continued through summer, fall, and early winter.

Pellet group counts conducted in the Chilcotin area indicated preferential use of sedge meadows and poplar forests by feral horses, but seasonal use could not be determined (Storrar et al., 1977). From aerial sightings, sedge meadows and south-facing grassy slopes appear to be among the preferred habitats of feral horses in the Yukon (D. Russell, pers. comm.) although degree and season of use of various types has not been quantified.

Snow Relationships

Snow cover is more or less complete during several months of the year in western and northern Canada, and as noted above, inability of feral horses to obtain adequate forage during deep snow years may be a mortality factor. During the study in western Alberta, horses appeared well able to cope with snow depths (average ~30 cm), encountered during mid- to late winter, and pawed snow as deep as 60 cm away from underlying forage. Although observed at all snow depths, pawing was resorted to more frequently in deep as compared to shallow snow cover (Table 3). Each pawing bout tended to involve more strokes in deep as compared to shallow snow, suggesting greater energy expenditure. Horses also were able to feed in shallow snow without pawing. In these situations, snow was 'plowed' away by pushing the muzzle through the snow at a selected spot, and subsequent snow clearing was accomplished by thrusting the muzzle forward while feeding. It appeared that this technique also was used to enlarge or clear snow from craters already created by pawing; it was used without pawing only at the shallowest snow depths (Table 4).

In addition to behavioral adaptations for feeding in snow, horses took advantage of reduced snow depths at tree bases in woods, and on hummocks and around shrub bases in open areas. Steep south-facing slopes remained snow-free or had reduced snow depth throughout the winter and also were exploited as feeding habitat.

Multiple tracks or trails were found in several habitat types; although trails appeared to be developed primarily in deep snow areas this relationship was not quantitatively examined.

Use of Shelter

Coniferous habitats found in western Alberta appeared to have high shelter value, but due to a low incidence of observations on the

use of shelter its importance could not be quantified. Winters during the study were exceptionally mild, however, and it is possible that shelter might be an important determinant of habitat selection during more severe periods. Conversely, meadow habitats, especially those with south-facing orientations, likely afforded favorable microclimates during fair weather and this may have been a factor in their utilization.

During the summer period horses were observed deep within wooded areas on a number of occasions, and frequently made use of shade at forest-meadow edges (including cattle salt-lick areas).

Food habits

Feral horses in western Alberta subsisted primarily on gramineous plants throughout the year (Table 5). Sedges, hairy wild rye, and fescues were the most important species; seasonal shifts in relative importance of each in the diet was probably related to both palatability and availability factors (Salter and Hudson, 1979).

Drinking

Areas frequented by feral horses in western and northern Canada are generally characterized by adequate sources of water, and it is unlikely that water supply is a major determinant of dispersion or habitat-use. Water was readily available from numerous streams during the study in western Alberta, and consequently horses did not gather at specific sites to drink as reported for more arid regions. Water requirements in winter were probably met largely by ingestion of snow.

Use of Mineral Licks

Feral horses, like other ungulates, make periodic visits to mineral licks. Horses in western Alberta ingested quantities of soil at both natural mineral licks and cattle salt licks throughout the year. Chemical analyses of soil, feces, and vegetation indicated that soil-eating likely was related to sodium deficiency (Salter and Pluth, in press).

Land-Use Conflicts

Land-use conflicts reported by management personnel during interviews and in the questionnaire surveys were competition for forage between horses and cattle, competition between horses and wild ungulates, and grazing and trampling damage on spring ranges. Reported problems were concentrated in areas with large horse populations, particularly where cattle-grazing is an important form of land use. Thus, feral horses in the central part of the Alberta foothills were reported to be competing with elk in winter and with cattle in summer, and to be overgrazing cattle allotments prior to the turn-out date (Salter, 1978b). In the Cariboo-Chilcotin area of central British Columbia, early season use of open hillsides was reported to result in range damage and forage competition (Salter and Hudson, 1978a). By contrast, feral horse populations elsewhere in the Alberta foothills, and in the northern part of the province, were not considered to represent serious land-use problems.

Studies conducted in western Alberta (Salter and Hudson, in press) provided additional insight into potential land-use conflicts. These studies documented some range damage as a result of grazing and trampling by horses in spring, and suggested the possibility of forage competition between feral horses and elk during winter and spring, depending on local population levels. Winter diets of horses and elk were 51% similar; both species fed in dry grassland habitat during winter and spring. The studies also showed that horses and cattle chose much the same diet (66% similarity during summer) and preferred some of the same habitats, resulting in overgrazing of dry grassland sites by fall. There was little indication of competition between horses and either deer or moose; horses ate little browse and habitat preferences were essentially different. Absence of competition between horses and moose also was suggested by the study in the Chilcotin area of British Columbia (Storrar et al., 1977).

Conclusions

The distribution of feral horses in western and northern Canada reflects both historic and current patterns of land-use--they are found in areas where, in the past, large numbers were allowed to stray or escape, and where present levels of management permit the existence of viable populations. They are currently confined largely to wilderness or semi-wilderness areas, where intensive management is difficult or significant land-use conflicts do not occur.

Present areas of concentration are characterized by coniferous forest cover and by relatively severe climate. Meadow (non-forested) vegetation types within the coniferous forest appear to be preferred habitats, although use is also made of forested types. Although forage selection has been studied in only one area of western Alberta, it is surmised (from observations on habitat preference) that feral horses depend primarily on gramineous plants throughout their range in western and northern Canada. Horses are able to feed in snow by pawing and by selecting feeding areas on the basis of snow depth, but the extent to which snow depth is a factor limiting mobility, habitat-use, and ultimately survival is not known. Availability of water is not considered to be a limiting factor.

Population dynamics of feral horse populations in western and northern Canada are not well understood. Limited quantitative evidence gathered in western Alberta suggested potential for rapid population growth, at least during mild winters and in the absence of predation and control of numbers through management. However, reports from management personnel and local residents indicated that mortality due to starvation may be high during severe winters--such die-offs have been reported from both British Columbia and Alberta, and in the absence of quantitative data over-winter mortality is considered to be the primary natural check on population growth.

Feral horses are thought to constitute land-use problems within parts of their range in western and northern Canada, but this has been adequately quantified in only one small area of western Alberta. At present, numbers of feral horses are being actively controlled in southern British Columbia in order to alleviate or prevent range-use

conflicts. Although round-ups have not been conducted in Alberta for several years, potential range-use conflicts in the foothills are being monitored and other types of free-ranging horses (primarily those owned by outfitters) are being controlled. Similarly, management personnel are attempting to collate information on numbers and distribution of feral and free-ranging outfitter horses in the Yukon, and to determine the extent of land-use conflicts. Assuming continued monitoring and control of feral horse numbers, populations in most areas of western and northern Canada are likely to decrease or remain relatively static in future.

Acknowledgements

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Table 1. Selected climatic characteristics of areas occupied by feral horses in western and northern Canada.[1]

	Mean daily maximum (°C)		Mean daily minimum (°C)		Mean annual snowfall (cm)
	Jan	Jul	Jan	Jul	
Western Alberta	-2	21	-19	4	218
Cariboo-Chilcotin	-3	23	-13	6	144
Southern Yukon	-15	20	-28	5	129

[1] From long-term measurements at Red Deer Ranger Station (western Alberta), Tatlayoko Lake (Cariboo-Chilcotin) and Haines Junction (southern Yukon). Data in Environment Canada, 1973a, 1973b.

Table 2. Seasonal distribution of horse sign by habitat type in western Alberta.

	Percent of total[2]		
Habitat type[1]	Winter sign (n=185)	Any age pellet groups (n=417)	Mean number[3] all age pellet groups per plot
Dwarf birch meadow	6.5 (5.3)	2.4 (2.4)	8.4
Mixed shrub meadow	11.4 (8.5)	7.0 (6.3)	8.3
Willow thicket	3.8 (2.6)	1.0 (1.6)	2.8
Dry grassland	9.7 (7.5)	4.8 (4.1)	4.4
Dwarf birch thicket	4.3 (3.2)	2.6 (2.2)	8.9
Mesic pine woods	0.5 (1.2)	... ...	...
Dry pine woods	$\underline{6.0}^{-}$ (14.4)	19.2 (20.4)	3.2
Black spruce woods	3.8 (3.0)	2.9 (2.4)	6.5
White spruce woods	$\underline{2.2}^{-}$ (7.1)	3.8 (4.3)	3.2
Poplar woods	$\underline{7.6}^{+}$ (4.2)	4.3 (3.9)	4.9
Mixed woods	14.0 (12.8)	18.4 (16.9)	4.2
Pine/alder thicket	27.0 (26.8)	31.4 (32.9)	3.2
Disturbed	0.5 (0.4)	0.7 (1.0)	4.0
Forested watercourse	2.7 (1.8)	1.4 (1.4)	3.3
Total χ^2	29.0	5.0	

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[1] Other habitats each comprising less than 0.5% of total area examined were sedge meadow, silver-berry thicket and alpine fir woods. Descriptions of habitat types are in Salter 1978a and Salter and Hudson 1978b.

[2] Based on presence/absence of tracks, feeding craters or pellet groups in 493 circular 15 m^2 plots examined Jan-Mar 1976 (winter sign) and of pellet groups in 490 circular 15 m^2 plots examined Jul-Aug 1976 (any age pellet groups). Percent of total plots sampled are in parentheses. Habitat types contributing 10% or more to significant total χ^2 values are underlined and marked + or - to signify preference or avoidance. Values of χ^2 at P=0.05 are 26.3 (winter) and 21.0 (any age).

[3] Based on counts conducted Jul-Aug 1976.

Table 3. Frequency of pawing by foraging horses in relation to snow depth, western Alberta.

Snow depth (cm)	Number of 5 min observations	Mean number of pawing bouts/ 5 min ± 1 s.d.	Mean number of strokes/pawing bout ± 1 s.d.
10	16	1.4 ± 2.0	5.4 ± 1.8
40-50	9	9.1 ± 3.8	9.7 ± 3.6

Table 4. Number of herd sightings during which pawing was used by foraging horses in relation to snow depth, western Alberta.

Number of observations involving:	Snow depth (cm)					
	1-10	11-20	21-30	31-40	40+	Total
Pawing	10	7	4	5	2	28
No pawing	6	2	0	0	0	8

Table 5. Major components of feral horse annual diets[1] in western Alberta.

Species	Percent composition
Grasses, sedges and rushes	93
Sedge (*Carex* spp.)	(34)
Hairy wild rye (*Elymus innovatus*)	(27)
Fescue (*Festuca* spp.)	(20)
Forbs	1
Browse	4
Miscellaneous (*Equisetum* spp., lichen, moss)	3

[1] Based on fecal fragments analysis of 12 monthly samples obtained during Jan-Dec 1976. Each sample was composited from subsamples of 50 fresh fecal groups.

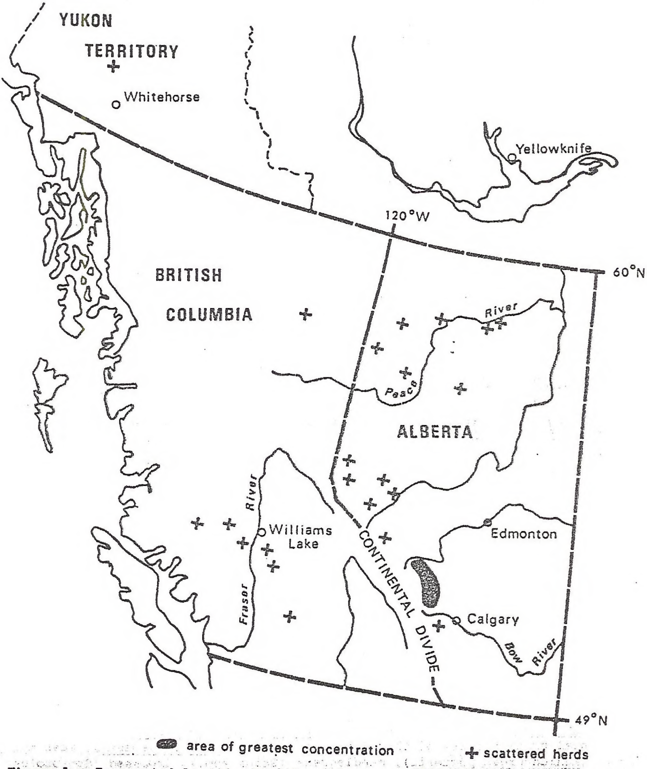
YUKON
TERRITORY
Whitehorse
Yellowknife
120°W
60°N
BRITISH
COLUMBIA
ALBERTA
Peace
River
Fraser
River
Williams
Lake
CONTINENTAL DIVIDE
Edmonton
Calgary
Bow
River
49°N
area of greatest concentration
scattered herds

Figure 1. Documented locations of feral horse populations in western and northern Canada. Feral horses may also occur in the northwestern third of British Columbia, in southern and central Yukon, and in the southwestern corner of the Northwest Territories, but the ownership status of horses occurring in these areas is unclear. Data from questionnaire surveys and interviews of Forest Service and wildlife management personnel, 1975-79.

Feral Burro Food Habits and Habitat Relations, Grand Canyon National Park, Arizona

Robert L. Potter and Richard M. Hansen
Department of Range Science, Colorado State University, Fort Collins

Abstract

The feral burro (Equus asinus) population in Grand Canyon has been periodically reduced by "burro hunts" between the 1920's and 1969. Experienced land managers seem to agree that heavy use by burros over many years has resulted in damage to vegetation in places. Presently (1968 to 1969), there are at least 300 burros in 116,000 acres of Park Service land at Grand Canyon. In August of 1977, food habits of burros were estimated by fecal analysis from ten study areas from about mile 80 to mile 110 of the Colorado River. Vegetation data from these ten study areas were collected the following spring. Diet composition for native herbivores was determined when their feces were present on an area. About one-fifth of burro and desert bighorn sheep (Ovis canadensis) diets, as well as about 30 percent of the relative herbaceous plant cover, consisted of one species of plant, foxtail chess (Bromus rubens), a common annual exotic grass of the desert Southwest. Diet overlap was estimated to be about 12 percent between burros and mule deer (Odocoileus hemionus), 44 percent between burros and desert bighorn sheep, and 40 percent between desert bighorn sheep and mule deer. Vegetation data when related to diet information indicates feral burros select plants most readily from habitat types also apparently important to desert bighorn sheep. In order to document alleged habitat destruction by feral burros in Grand Canyon National Park, we feel the Park Service should construct grazing exclosures.

Introduction

Feral burros (Equus asinus) are believed to be native to northeastern Africa and to have been first introduced to the southwestern United States in the 16th century by Spanish explorers. Burros were important pack animals to these early explorers and were also important in the opening of the entire western United States. Eventually some burros escaped captivity and did quite well on the native vegetation. Miners around the mid- to late 19th century entered Grand Canyon, not yet a national park, and brought along their burros to carry in supplies and to carry out finds. Few mineral finds in the canyon proved profitable, and the miners often turned their burros loose when they were no longer needed. Thus was the start of the feral burro problem.

McKnight (1958) estimated from National Park Service (NPS) records that there were 1,500 to 2,000 burros in Grand Canyon. In a press release (The Grand Canyon Guide, August 1977), the NPS reported that burros numbered 500 to 1000 in the Park and had increased at an annual rate of 20 percent since 1969, when public sentiment stopped control efforts. A helicopter mark-and-observe study conducted the same year determined for the first time a confident estimate of burro numbers, about 300. In the period from 1924 to 1968, 2,608 burros were killed by the NPS in periodic "burro hunts." If we assume an average annual kill rate of about 15 per-

cent plus a natural mortality rate of 5 percent, a healthy expanding population of 300 burros could easily account for the harvest records. Therefore, it seems reasonable to assume, overall, that Grand Canyon National Park has received near constant pressure from burros since its inception.

The purpose of this study was to determine the food habits of feral burros by fecal analysis and examine, with the aid of vegetation data, habitat preferences. Also, we tried to determine to what degree burros compete for food with native large herbivores in Grand Canyon National Park.

Study Area

Food habits of feral burros were studied and vegetation data were collected from about river mile 80 to 110 of the Colorado River in Grand Canyon National Park, Arizona. An attempt was made to determine food habits of desert bighorn sheep (*Ovis canadensis*) and mule deer (*Odocoileus hemionus*) from the same areas. The ten study areas were Red Canyon (RC), Mineral Canyon (Mi), Cottonwood Canyon (Ct), Grapevine Canyon (Gv), Pipe Springs (PS), Indian Garden (IG), Monument Canyon (Mn), Boucher Canyon (Bc), Turquoise Canyon (Tq), and Copper Canyon (Cp). The use of symbols for the study areas in the text and figures was adopted for brevity.

The study areas are within the boundaries of Grand Canyon National Park, which is located entirely in the northern portion of Arizona. The Park represents some 1,226,656 acres (496,410 hectares) of Mohave and Coconino counties, Arizona. The ten areas we studied are dispersed along the south side of the Colorado River and are in Coconino County.

The Grand Canyon is part of the physiographic region known as the Colorado Plateau of the Plateau Province, which includes parts of Colorado, New Mexico, Utah, and most of northern Arizona, generally following the lower parts of the Colorado River drainage. This Province is characterized by high mesas and deep canyons with precipitous cliffs, making any type of ground travel difficult. Topography of the study areas consists of rugged, steep-walled canyons that empty into the Colorado River.

Below the rim of the canyon, the temperature is extreme in the summer months, July being the hottest. Winter months are mild, and freezing temperatures are uncommon. Summer is also the wettest period in the canyon, with most of the precipitation occurring as severe thundershowers. Rainfall amounts are generally below 8 inches (200 mm) annually (NPS, 1979).

Vegetation on the study sites is considered by Brown et al. (1977) to be within the Great Basin desertscrub zone, with some intermixing of plants from the Mohave desertscrub zone. The latter zone occurs as a thin band along the floor of the canyon adjacent to the Colorado River for much of the length of the Park. At this interface of the two zones, the dominant shrub is blackbrush (*Coleogyne ramosissima*), with common associates being wolfberry (*Lycium pallidum*), sagebrush (*Artemisia* spp.), Mormon tea (*Ephedra* spp.), and snakeweed (*Xanthocephalum sarothrae*). Common perennial grass species of this zone are galleta (*Hilaria jamesii*), bush muhly (*Muhlenbergia porterii*), needlegrass (*Stipa* spp.), dropseed (*Sporobolus* spp.), and lovegrass (*Eragrostis* spp.). Common perennial forb species include globemallow (*Sphaeralcea* spp.), bedstraw (*Gallium* spp.), hymenoxys (*Hymenoxys* spp.), and beardstongue (*Penstemon* spp.). Plants from the Mohave desertscrub zone that commonly intermix with the Great Basin desertscrub zone include Utah agave (*Agave utahensis*), white brittlebush (*Encelia*

farinosa), pricklypear (Opuntia spp.), and catclaw acacia (Acacia greggii).

Another important and dynamic part of the desert community comprises annuals, which can, in years of favorable weather, overshadow other components of herbaceous plants. Important annual grasses are foxtail chess (Bromus rubens), cheatgrass (Bromus tectorum), sixweek fescue (Vulpia octoflora), and annual bluegrass (Poa annua). Important annual forbs are milkvetch (Astragalus spp.), wildbuckwheat (Eriogonum spp.), sandwort (Arenaria spp.), and pepperweed (Lepidium spp.).

Within the canyon occur numerous springs and seeps along with perennial streams, which give rise to another important component of the desert ecosystem, the riparian habitat. These local areas are very diverse and can vary dramatically within a few meters. Commonly, there is a large tree and shrub component along with a greater diversity of herbaceous plants than found in the adjacent desertscrub community. Overstory species in this type include cottonwoods (Populus spp.), seepwillow (Baccharis glutinosa), willow (Salix spp.), willow weed (Epilobium spp.), Apache-plume (Fallugia paradoxa), and an occasional ash (Fraxinus spp.). Herbaceous species include those listed for the desertscrub community plus Bermuda grass (Cynodon dactylon), sedges (Carex spp.), rushes (Juncus spp.), cattail (Typha spp.), rabbitfoot grass (Polypogon monspeliensis), and many others.

Procedures and Methods

The fecal materials used for determining the botanical composition of the diets of burros, desert bighorn sheep, and mule deer were obtained in late August 1977. The areas were selected in advance with the help of personnel of the NPS and travel to the areas was by helicopter. The samples were found along the trails next to the "bedding grounds" of burros. There was an abundant supply of burro feces, varying in age from fresh to probably several years old. A two-gram sample of each of 36 different defecations (piles) was obtained from each of the ten study areas. One pellet per pellet group was collected whenever the defecations of desert bighorn sheep amd mule deer were encountered. The number of sheep or deer pellets analyzed varied from none on four study areas to 47 from Mn (Table 1). The fecal material was collected without bias toward freshness, and we assume that the estimated diets represented annual food consumption from the areas.

The fecal samples were examined by the microhistological examination of plant fragments left intact after digestion. The use of this technique permits the study of interactive food habits without the slaughter of animals and has become, in recent years, an acceptable method of quantifying plants in the diets of herbivores (Dearden et al., 1972; Flinders and Hansen, 1972; Hansen and Clark, 1977). Each individual burro defecation was examined by making one slide per defecation and examining 20 fields per slide at 100x. Frequency of occurrence in the microscope fields was converted to relative density by the procedure described by Sparks and Malecheck (1968).

Each sheep and deer pellet was microhistologically analyzed at the same intensity as each burro defecation. These estimated compositions were subjected to hierarchical anlaysis based on similarity in order to classify them by the native herbivore, mule deer, or desert bighorn sheep, from which they may have originated. Clusters of similar pellets were subjectively assigned to "deer-like" or "sheep-like," based on botanical composition. The number of pellets examined from each study area on which at least one pellet was found and the number assigned to desert bighorn

sheep or mule deer varied (Table 1).

In the latter part of May 1978, vegetation records were collected from transects at the same ten areas where fecal material had been collected. Upon hiking into each side canyon, field collectors visually stratified the area into three broad habitat types: 1) blackbrush, 2) riparian, and 3) sideslope. The blackbrush habitat type, which is by far the most extensive, occurs on a large shelf known as the Tonto Platform, about halfway down from the rim of Grand Canyon to the Colorado River. The riparian type, which was represented in most areas, was considered to be the narrow band of stream-side vegetation, generally less than 25 to 50 meters wide. The third type consisted of the talus slopes and nonriparian vegetation of the side canyons. This type appeared to be distinct in both shrub and herbaceous components. A large transition between the blackbrush type and this type generally occurred at the mouths of each side canyon and care was taken to avoid sampling in this transition. A fourth type, sampled only in Cp, was a pinyon-juniper community. This was also the only type sampled in Cp.

An attempt was made to sample each of the three major types in each study area, but this was not always possible, because of lack of time or absence of one or more of the types in a given area. In Rc and Mi, only the sideslope type was sampled, with one stand in each area. In Gv, Tq, IG, and PS, one stand per type was sampled in each area. Ct was sampled with two blackbrush stands and one each of the other two major types. Stands in Mn were two blackbrush, two riparian, and one in the sideslope type. In Bc, two sideslope stands and one in each of the other two types were sampled. Collectively, nine blackbrush, eight riparian, and ten sideslope stands, for a total of 28 vegetation stands, were sampled.

Vegetation records were obtained in all but the riparian type using line intercept and Daubenmire cover class estimation (Mueller-Dombois and Ellenberg, 1974) in 20 x 20 cm quadrats, for shrub overstory canopy cover and ground cover of herbaceous species, respectively. Each stand sampled consisted of three or five 50-meter transects, with ten systematically placed quadrats at five-meter intervals along the transect. Centimeters of intercept were recorded by species and a one to six cover class rating was recorded for each species that occurred in each quadrat. In the riparian type, the same estimation procedures were used, but the transects were shortened to 15 meters and 15 quadrat placements were recorded at one-meter intervals. This modification was needed, since seldom did this type reach a width of 50 meters. Five transects were recorded in all of the riparian stands except as noted below for the Indian Garden stand. We attempted to sample this type adjacent to, or in close proximity to, free water.

The riparian type at the Indian Garden study area, which was sampled just below Indian Garden campground, was markedly different from the other riparian stands. The cover was very dense with numerous large trees, thus prohibiting the use of transect methods. We sampled this stand using ocular estimates of total cover for overstory and understory, then we would partition the cover by species on a relative basis. Fifty estimates were made at 50-meter intervals along Garden Creek. Garden Creek is one of several major perennial streams in Grand Canyon and is situated in an area of high burro concentration.

Similarity indexes were used to compare herbivore diets within areas and to compare vegetation stands of the same type between areas. This measure, commonly called Sorenson's index of similarity, estimates the proportion of the mean botanical compositions of a pair of diets or stands

that is identical. A one-dimensional ordination procedure based on similarity was used to study the relationships among diets and stands in this study (Mueller-Dombois and Ellenberg, 1974).

Results

When the mean compositions of burro defecations from all ten areas are averaged (Table 2), a marked preference for grasses was observed. Of 19 plant taxa averaging greater than 1%, 12 are grasses, three are forbs and four are shrubs. Major grasses are brome (Bromus spp.) (18%), galleta (8%), and Bermuda grass (7%), bush muhly (6%), needlegrass and dropseed (5% each), with grasses totaling about 66% of the diet. Major forbs are pricklypear (9%), wildbuckwheat (5%), and globemallow (1%); forbs amount to about 16% of the diet. Two shrubs, sagebrush and Mormon tea, averaged 4% and 3%, respectively, with shrub components totaling to 11% of the estimated average annual diet. Estimated mule deer diet compositions averaged across six areas show that two grasses, one forb, and nine shrubs plus seed constitute more than 1%. Grasses were brome (1%) and bluegrass (Poa spp., 1%), with globemallow (3%) being the only forb of significance. Major shrubs in mule deer diets include saltbush (22%), Mexican cliffrose (Cowania mexicana, 15%), blackbrush (15%), greasebrush (Glossepetalon nevadensis, 10%), snowberry (Symphoricarpos spp., 10%), garrya (Garrya spp., 5%), and Mormon tea (3%); totally, shrubs compose about 84% of the estimated annual deer diet. Averaging compositions of pellets classified as desert bighorn sheep across four areas shows eight grasses, one forb, and seven shrubs compose greater than 1% of the botanical composition of the diet. Important grasses are brome (20%), bluegrass (10%), dropseed (5%), galleta (4%), Bermuda grass (3%), ricegrass (3%), and bush muhly (2%), with grasses collectively composing nearly 52%. Again, as in the mule deer diets, globemallow (2%) is the only forb composing greater than 1%. The shrub component of desert bighorn sheep includes saltbush (13%), blackbrush (8%), garrya (5%), sagebrush and Mexican cliffrose (4% each), and greasebush (3%), and the shrub component amounts to 40%.

When mean diets for burros are examined for each study area, the Bc area is the only site differing greatly from the rest. Bermuda grass composed 95% of the relative herbaceous cover and composed over 73% of the diet of burros at Bc. The only other notable difference between burro diets was the large proportion of brome (45%) in Gv. Most burro diets were at least 50% similar between study areas, generally reflecting varying proportions of brome, bush muhly, galleta, pricklypear, wildbuckwheat, sagebrush, and Mormon tea.

Brome exceeded 24% only in Gv and was a major dietary component (13-24%) in the remaining areas except Bc (4%). Galleta varied from 1% at Tq and Bc to 18% at Mi, 20% at Cp, with the remaining burro diets varying from 2 - 9%. Bermuda grass was a major dietary component only in Bc (73%) and was 1% or less in all other areas. Bush muhly was highest in Cp(11%), followed by Mn (10%), and ranged from 2 - 7% in the other areas. Needlegrass was important to burros in PS (11%), IG (11%), and Mn (8%) and varied from less than 1 - 6% in the remaining diets. Dropseed was important to burros in Mn (13%), IG (10%), Ct (9%), and Cp (6%) but relatively minor (1 - 4%) in the other areas. Pricklypear was a large proportion of the composition in Tq (20%), RC (17%), Mi (14%), IG (10%), PS and Ct (8% each), and Gv (6%) but a minor component in other areas. Wildbuckwheat was a consistent food for burros in all areas, averaging 2 - 10%, with PS and Tq

(10%) being highest and Ct, Bc, and Gv (2%) having the lowest amounts. Globemallow was present in generally low amounts in all diets except Tq (4%) and Cp (3%). Sagebrush was greater than 5% only in PS (11%) and Cp (6%). Mormon tea varied from less than 1% in Bc, Cp, and IG, averaging 3-8% in the burro diets from the other study areas.

Mule deer diets from six areas varied greatly in composition for major and minor plant species. The IG, Mn, and Bc deer diets were very similar, but the diets from the other study areas were much less alike. Desert bighorn sheep diets discerned from four areas showed a high degree of similarity to each other.

The similarity between feral burro and mule deer diets on six areas averaged 12% (IG = 6%; Gv, Mn, and Bc 7% at each area; PS = 12%; Tq = 34%). Diet overlaps averaged 44% between feral burros and desert bighorn sheep (Bc = 31%; PS = 36%; Tq = 48%; and Mn = 62%). The overlaps between mule deer and desert bighorn sheep on four areas averaged 40% (Mn = 27%; PS = 37%; Bc = 39%; Tq = 56%).

The overstory canopy coverage of the woody vegetation (shrubs plus trees) averaged significantly higher in the riparian stands (44%) than in the blackbrush (23%) or sideslope (21%) stands of the Tonto Plateau. The herbaceous ground cover averaged 8% among the three habitat types (excluding Cp). The vegetation cover of the pinyon-juniper stands of Cp were not like the others. At Cp the woody canopy coverage averaged 10% and the herbaceous coverage 16%. No single plant species occurred in all the stands as a major component, and stands were generally representative of local conditions on the sampling site (Tables 3 and 4).

The similarity was high for the botanical compositions of stands in the blackbrush type. Relative canopy coverage of woody plants averaged 90% for blackbrush, Mormon tea 6%, and the other shrubs averaged 1% or less (Table 3). Relative ground cover of herbs in the blackbrush type averaged 36% for annual grasses (sixweek fescue, 18%; brome, 13%; annual bluegrass, 5%), 22% for the three most common annual forbs (milkvetch, 10%; filaree, 6%; lupine, 6%), and Cactaceae averaged 8% (Table 4).

Botanical similarity of the sideslope stand was intermediate , and the riparian habitat varied the greatest between stands. Relative canopy coverage of woody plants on the sideslopes averaged 42% for Mormon tea, 34% for snakeweed, 9% for haplopappus (Haplopappus spp.) and 6% for wolfberry. A variety of herbs averaged more than 1% of the relative ground cover (Table 4), and the most important taxa were brome (28%), sixweek fescue (10%), and milkvetch (11%).

The botanical compositions of the riparian stands had the highest diversity, greatest biomass, and the largest differences between stands for the habitat types studied. There were 14 woody plants whose relative canopy coverage averaged more than 2%. Major plants were willow (20%), seepwillow (Baccharis spp., 16%), cottonwood (16%), desert willow (Chilopsis linearis, 10%), and Apache-plume (5%). The relative herbaceous ground cover in the riparian stands averaged 31% for brome and 5% each for dropseed and sixweek fescue. Bermuda grass was 95% of the ground cover in Bc and of minor importance in the other study areas. The diversity of forbs was high in the riparian stands, but the only species to contribute 3% or more to the relative ground coverage was milkvetch, which averaged 3%.

The relative cover of woody plants in the pinyon-juniper stand sampled in the Cp area was characterized by Fremont's mahonia (Mahonia fremontii, 20%) snakeweed (29%), roundleaf buffaloberry (Shepherdia rotundifolia, 17%), and Mormon tea (10%). Minor components were wavyleaf

oak (Quercus undulata) and yucca (6% each) and Mexican cliffrose (2%). The relative coverage of herbaceous plants in Cp was primarily sixweek fescue (15%), galleta (9%), brome (8%), bottletail squirreltail (Sitanion hystrix, 2%) grama grass (Bouteloua spp., 2%) Cactaceae (14%) and desert Indianwheat (3%). Together, hymenoxys and hymenopappus (Hymenopappus spp.) made up 13% of the relative herbaceous cover.

Discussion

Feral burros inhabiting the desertscrub community in Grand Canyon National Park consume primarily grasses (66%); second, forbs (16%); and last shrubs (11%). These estimates of annual diet components are in close agreement with those determined from the Grand Wash Cliffs area by Hansen and Martin (1973), where feral burros also consumed primarily grasses (68%); then forbs (14%); and last, shrubs (13%). The area studied by Hansen and Martin (1973) was in the Mohave desertscrub zone. Woodward and Omart (1976) studied feral burros diets in the lower Colorado River subdivision of the Sonoran desertscrub (Brown et al., 1977), but in that study shrubs composed most of the diet (61%), followed by forbs (30%), with grasses only a minor component (4%). Hanley and Brady (1977) determined browse utilization as a function of distance from the Colorado River in a study area adjacent to Woodward and Omart's (1976). They concluded that utilization was significantly higher within 2.4 miles (1.5 kilometers) of the Colorado River but was not significantly different at greater distances. In Death Valley National Monument, Browning (1960) determined that feral burros consumed primarily shrubs (51%); then forbs (39%); and last, grasses (10%). This evidence leads to the conclusion that burros are highly adaptable and consume whatever plants are most palatable. Our data and that of Hansen and Martin (1973) indicate that grasses are preferred by burros, but that when unavailable, shrubs and forbs are readily consumed.

Feces of mule deer and desert bighorn sheep are not distinguishable to most biologists. The method used to separate the feces into two mutually exclusive groups was an agglomerative information analysis (Poole, 1974), a standard ordination technique that seems to be most appropriate to this problem. A possible alternative would be a presence-absence divisive method but would require prior knowledge of indicator species, that is, species consumed by one group but not by the other. Because this study represents the only information collected in Grand Canyon on food habits of mule deer and desert bighorn sheep, such information is nonexistent. Thus, the method used is the best approximation available.

One aspect of the classification that needs mentioning is the apparent bias towards mule deer (2.2:1 mule deer to desert bighorn sheep ratio, Table 1) of the pellets classified. Population numbers of desert bighorn sheep in Grand Canyon are very low, but their distribution is thought to be throughout all ten areas we studied, while mule deer presence below the rim is termed only occasional (NPS, 1979). Two causes for this bias are possible. First, locations where fecal samples were collected were generally near the bottoms of the side canyons along the washes, generally in areas mule deer would spend most of their time feeding and resting, while sightings of desert bighorn sheep indicate that they spend most of their time on the precipitous cliffs of the Redwall Formation and would frequent the washes only when watering. Second, some of the pellets classified as originating from mule deer may be in fact feces of desert bighorn sheep. Clusters of similar pellets were assigned to "sheep-like" if they contained substantial proportions of grasses, a characteristic

normally associated with desert bighorn sheep diets, and assigned to "deer-like" if they contained primarily shrubs, since mule deer are generally thought to be browsers by preference. But, in winter, when grasses are least available, desert bighorn sheep could possibly consume shrubs to meet nutritional requirements. If the second case were true, it would only serve to lower the magnitude of diet overlap with feral burros. Thus, we can consider our estimates of annual diet overlap between feral burros and desert bighorn sheep to be an upper limit. Future research goals of the NPS should include determination of confident estimates of mule deer and desert bighorn sheep diets on a seasonal basis.

Annual diet overlap on six areas for feral burros and mule deer indicates that competition for food is not great, with the possible exception of the Tq study area (34%). Annual diet overlap between feral burros and desert sheep on four areas, however, suggest possible conflicts could exist on all areas, with potential competition being greatest at Mn (62%). The level of overlap that implies competition is, though, a subjective matter. Also, when only annual diets are compared, local and seasonal situations of potential competition are ignored.

Habitat data when compared to food habits information suggest that the sideslope habitat type likely is the most important to feral burros, where they take primarily perennial grasses. The riparian type follows closely because of high proportions of grasses, while the blackbrush habitat type appears to be used for Cactaceae and wildbuckwheat diet components. Brome grass is readily available in all habitat types but may be quite seasonal in its palatability because of the ephemeral nature of its growth. Mule deer alternatively select the riparian habitat most often for feeding because of the presence of the most preferred shrubs only in this type. The blackbrush type is next most preferred because of the blackbrush component of the diet, with sideslope plants other than Mormon tea being least important. Of the habitat types we sampled, desert bighorn sheep appear, as did feral burros, to select plants that are most abundant in the sideslope habitat type. The blackbrush habitat would likely be next most preferred, with the riparian type least favored.

Two other important habitat types are present at these localities in the Park, the Colorado River riparian and the precipitous cliffs that desert bighorn sheep apparently frequent, as evidenced by rare sightings. All three herbivores apparently use the Colorado River riparian because of the presence of mesquite (Prosopis juliflora) in the diet information and since this plant appeared to be limited in its distribution to this type. The precipitous cliffs of the Redwall Formation are of undetermined value but could possibly be a significant source of perennial grasses to desert bighorn sheep but unavailable to burros.

Woodward and Ohmart (1976) determined habitat preferences of feral burros seasonally by observation for the Chemehuevi Mountains of eastern California in a Sonoran vegetation type. Their study indicated that the Colorado River riparian was used only intermittently in mid- to late summer, while major washes leading to the river were used most from early summer into late fall. Desert bajadas (roughly corresponding to our blackbrush type) were the main source of annual forbs as well as typical Sonoran desert shrubs, which composed a majority of the feral burro diet in that study.

Park Service policy dictates removal of all exotic species when possible. Current Park Service estimates are that about 9.5% of Grand Canyon National Park is impacted by feral burros. The question arises: Are burro populations currently at a level that cannot be sustained by the Park's natural and exotic plant communities? Let us take as our

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Table 1. Number of pellets assigned to desert bighorn sheep (*Ovis canadensis*) and mule deer (*Odocoileus hemionus*) by hierarchical analysis based on similarities and number of pellets in which no discernible plant fragments were found, collected from six study areas in Grand Canyon National Park, Arizona, in late August, 1977.

Study Area	No. of pellets assigned to desert bighorn sheep	No. of pellets assigned to mule deer	No. of pellets in which plant fragments were not discernible	Total no. of pellets examined on each area
Grapevine Canyon	0	33	0	33
Pipe Springs	9	26	1	36
Indian Garden	0	25	2	27
Monument Canyon	18	28	1	47
Boucher Canyon	5	15	1	21
Turquoise Canyon	31	11	1	43
Total assigned to each category	63	138	6	207

Table 2. Percent relative density of plant fragments found in feces of native and exotic herbivores in Grand Canyon National Park, Arizona, collected in late August 1977. Parenthetical numbers represent how many areas over which mean compositions were averaged.

Plant taxa	feral burros (10)	mule deer (6)	desert bighorn sheep (4)
Grasses			
Agropyron spp	2	< 1	1
Aristida spp	3	< 1	1
Bouteloua spp	4		1
Bromus spp	18	1	20
Cynodon dactylon	7		3
Hilaria jamesii	8	< 1	4
Muhlenbergia porteri	6	< 1	2
Poa spp	3	1	10
Sporobolus spp	5		5
Oryzopsis hymenonis	4	< 1	3
Stipa spp	5	< 1	2
Tridens spp	1		< 1
subtotal	66	3	52
Forbs			
Eriogonum spp	6	< 1	1
Opuntia spp	9	< 1	< 1
Sphaeralcea spp	1	3	2
subtotal	16	3	3
Shrubs			
Artemisia spp	4	2	4
Atriplex spp	< 1	22	13
Coleogyne ramosissima	1	15	8
Cowania mexicana	< 1	15	4
Ephedra spp	3	3	1
Garrya spp	< 1	5	5
Glossepetalon nevadensis	2	10	3
Prosopis juliflora	1	2	2
Symphoricarpos spp	< 1	10	< 1
subtotal	11	84	40
Miscellaneous			
seed	< 1	1	1
unknown	< 1	1	< 1
others	7	8	4
subtotal	8	10	5
Total	100	100	100

Table 3. Relative percent canopy cover of shrubs estimated by line intercept methods in four habitat types sampled in late May 1978 at Grand Canyon National Park, Arizona. Parenthetical numbers represent how many stands over which mean compositions were averaged.

Plant taxa	Habitat Types			
	Blackbrush(10)	Riparian(8)	Sideslope(10)	Pinyon-Juniper(1)
Artemisia spp		<1	2	
Atriplex spp			1	
Cercis occidentalis		2		
Cercocarpus spp		2		
Chilopsis linearis		10		
Coleogyne ramosissima	85		1	
dead	5			
Cowania mexicana		2	<1	2
Ephedra spp	6	1	40	10
dead	1	<1	2	
Baccharis spp		15		
dead		2		
Fallugia paradoxa		5	<1	
Xanthocephalum sarothrae	<1	4	29	25
dead		<1	5	3
Haplopappus spp	<1	<1	9	
Juniper spp		1		
Lycium pallidum	1		6	
Mahonia fremontii		1		
Populus spp		16		
Quercus undulata				6
Rubus procerus		2		
Rhus trilobata var. simplicifolia		4	1	
Salix spp		20		
Shepherdia rotundifolia				17
Stanleya pinnata		4		
Tamarix pentandra		1		
Unknown shrub		3		
Vitis arizonica		1		
Yucca spp	1	<1		6
Others	1	4	4	1

Table 4. Relative percent cover of herbaceous plant species estimated by Daubenmire cover class estimation methods in four habitat types sampled in late May 1978 at Grand Canyon National Park, Arizona. Parenthetical numbers represent how many stands over which mean compositions were averaged.

	Habitat Types			
Plant taxa	Blackbrush (9)	Riparian (8)	Sideslope (10)	Pinyon-Juniper (1)
Grasses				
Bouteloua spp				2
Bromus spp	13	31	28	8
Cynodon dactylon		10		
Hilaria jamesii	< 1	< 1	1	9
Muhlenbergia porteri			2	
Poa spp	5	2	2	< 1
Polypogon monspeliensis		6		
Sitanion hystrix		1		
Sporobolus spp		5		
Stipa spp		< 1	3	
Unknown grass			< 1	
Vulpia octoflora	18	5	10	15
Grass likes				
Carex spp		2		
Juncus		1		
Forbs				
Astragalus spp	10	3	11	
CACTACEAE	8		1	14
Calochortus spp	2		1	
Cryptantha spp	1	1	1	< 1
Dyssodia spp			1	
Erodium cicutarium	6	< 1	2	
Gallium munzii		1	1	
Hymenoxys - Hymenopappus				13
Lepidium densiflorum	1	1	2	
Lupine spp	6			
Mentzelia spp	1			
Tortula	9		5	
Plantago insularis	1	< 1	1	3
Rorippa spp		2		
Sisymbrium spp	2	1	1	
Sphaeralcea spp	< 1	< 1	1	
Unknown forbs	17	21	22	33
Others	< 1	6	1	

Strategies of Feeding Behaviour in the Common Zebra *Equus burchelli* (Gray) in Amboseli National Park, Kenya

Christopher G. Gakahu
Department of Zoology, University of Nairobi, Kenya

Abstract

The study was conducted from May 1977 to September 1978 in Amboseli National Park along the Kenya-Tanzania border to the north of Mount Kilimanjaro. The study area is naturally defined by the Amboseli basin, which was a Pleistocene lake that dried up and became colonized by vegetation. Permanent swamps, woodlands, and open grass plains are the main vegetation types in the basin.

During the rains migratory herbivores, mainly zebra and wildebeest, move out of the basin to wet season dispersal areas. While the herbivores are away, grass which had been grazed almost to ground level (under 10 g./m^2 in the open plains) grows to over 200 g./m^2 in most areas. In the dry season the herbivores return to the basin and first occupy the plains, then the woodland, and finally the swamps. This phenomenon makes the basin a dry season concentration area. The return of the animals to the basin is mainly due to lack of surface water, in the wet range, which is readily available in the swamps. Why the animals move out of the basin is still under investigation, but results to date indicate that grass in the dispersion area is less coarse and of higher quality (crude protein level). Thus the animals select habitats of optimum quality and quantity of forage.

The hypothesis put forward is that zebra feeding behaviour is related to food availability. When standing crop is high, animals may be expected to spend less time feeding compared to periods of low-standing crop; i.e. to harvest an equivalent quantity of forage more time is required.

Progression rates (while feeding) and activity patterns of zebra were quantified during the wet and the dry seasons. Progression rates were significantly dependent on standing crop (in g./m^2). When standing crop was low, more time was spent moving to the next feeding point and vice versa.

Zebra adjusted the time allocation to various activities according to the amount of food available. More time was spent grazing during the dry than the wet season, when social activities were more common.

Habitat Preferences of Africa's Recent Equidae, with Special Reference to the Extinct Quagga

Elizabeth Cary Mungall, Affiliate of College Eight, University of California at Santa Cruz

Abstract

The habitat preferences of Africa's recent Equidae are discussed. These equids are characteristic of relatively dry habitats: grassland, savanna, thorn scrub, Cape macchia, karroo, and desert. Even though earliest records from different regions span several centuries during which time some populations have become extinct, mapping of maximum historical distributions emphasizes several important features; most importantly, each species is adapted for a different vegetation type, and as these vegetation types grade into one another the associated equids show a zone of overlap. The African wild ass fits into the same overlap scheme as the zebra species.

Despite the extinct quagga's obviously close relationship with the zebras of the Burchell's group, the quagga's correlation with the distinctive karroo vegetation supports impressions of contemporary observers that this form was a separate species. A new scientific name, Equus asinus atlas, is proposed for the Atlas wild ass since the identity of its type fossil has been challenged.

Introduction

On the African continent, species overlap is a prominent theme in equid distribution. Mapping the distributional limits for Africa's zebras and wild asses, one finds close correlations between area inhabited and vegetation type.

A feature which has retarded a coordinated realization of this overlap scheme is the vast extent of space and time which must be considered. Earliest historical records of its fauna come at widely different periods for different regions. Saharan rock art links our knowledge with an evolutionary past when conditions allowed eland, giraffe, and elephant to roam what is now desert. Ancient Roman writings describe species from northern Africa that vanished before modern science developed. Linnaeus and his contemporaries laid the foundation for sorting out the multitude of species being described as a new wave of colonization swept deeper into Africa.

Problems of species overlap came in at least as early as Linnaeus' mistaken impression that the quagga was the female of the mountain zebra. Understandably, the emphasis from the 1600's through the 1800's as new species and subspecies were discovered was on separation. Now that a comprehensive and workable taxonomic structure for Africa's larger mammals is well established, emphasis has shifted to ecological relationships. Thus, the overlap areas which caused early naturalists such confusion can be studied in a new perspective. For maximum effectiveness, this effort should encompass the whole continent so that the entire network of overlap zones can be considered together. Immediately one thinks of the zebra species including the extinct quagga, but North Africa's wild asses should also be included. Modern science has come to recognize that coat color differences can be superficial when a wider range of characters is evaluated. Why should the African wild ass be thought of as more different from the zebras than the zebras are from each other?

Results and Discussion

African wild ass, *Equus asinus*

Africa's wild asses inhabit the hottest and driest regions frequented by any of the continent's *Equus* species. As shown by comparing a distribution map with a vegetation map (Figs. 1 and 2), these asses occur principally in semi-desert and desert areas. Their range includes the Danakil Depression. This volcanic zone at the crossroads of three rift areas has subsided to a maximum of 120 m below sea level since the time it was an arm of the Red Sea. Rock temperatures in the Danakil can reach 160°C; air temperatures often climb to 57°C (Willock et al., 1974). Into this desolate region, the Awash River flows, cutting a steep gorge with 100 m of grass and acacias along each bank (Willock et al., 1974).

In the Danakil as well as elsewhere, asses moderate the environmental conditions they actually experience by selecting low stony hills, high plateaus, wadis, major watercourses, and coastal plains. While frequenting dune areas, they avoid soft sand (Harper, 1945; Tate, 1971). They use plains dotted with grass clumps and thorn forests with aloe undergrowth (Sidney, 1965). During summer when temperatures can exceed 50°C, asses often shelter by the sparse vegetation from 1000 to 1700 hr, then graze with a trip to water during the night (Groves, 1974). Summer grass is dry and hard, but winter grazing offers the asses enough moisture so that they can go two or three days without drinking (Tate, 1971).

Consistent with their arid habitat, African wild asses are highly mobile, penetrating far into the desert when rains spur plant growth. Population densities are low, especially during summer when the animals scatter in search of water (Harper, 1945; Tate, 1971). Their irregular movements and low density plus the inhospitable nature of their homelands make defining distributional limits particularly difficult. Low numbers and clumped distribution of observations add to the problem.

Another difficulty is proximity to civilizations that reached a high level of development in very early times. Art work at the temple of Medinet Habu shows the pharaoh, Rameses III, who reigned from 1198 to 1167 B.C., hunting wild asses; Antonius maintains that, as late as 1100 B.C., the ass was a well-known wildlife species in Egypt (Antonius in Harper, 1945). Concurrently, domesticated asses were laboring for Egyptian masters. The ancient Egyptians had domesticated Nubian stock as early as 3500 B.C. (Antonius in Harper, 1945). In modern times, only occasional rains have been noted to lure wild asses into Egypt (Harper, 1945). Semantic problems due to shifting political boundaries compound the uncertainty. The fifth century Greek historian Herodotus, who had resided for a long time in Egypt as part of his travels, lists asses among the wild animals of "Libya," ancient name for the region from the west bank of the Nile to the Atlantic Ocean (Ridgeway, 1905).

Roman control skirted inland of North Africa's Atlas Mountains by 117 A.D. Although gone by modern times, there apparently was then a distinctive type of wild ass inhabiting the foothills. A rock picture at Enfouss in what is now northern Algeria shows an ass resembling the Somali wild ass, E. a. somaliensis, in having striped legs and the Nubian wild ass, E. a. africanus, in having a well developed shoulder cross. A large hunt scene discovered in a Roman villa at Hippo Regius (now Bone, Algeria) includes the chase of an ass marked like that at Enfouss. With this in mind, Werth (in Harper, 1945) described the Atlas wild ass as a distinct subspecies of Equus asinus. He designated it atlanticus, using the name P. Thomas had given in 1884 to a mandible from late Pleistocene deposits at Oued Seguen, Algeria. However, Groves (1974) points out that recent reevaluation of the atlanticus fossil has determined it to represent a zebra. Pending resolution of this question, the present author proposes to call this ass Equus asinus atlas after the assumed homeland of the animal. The Roman mosaic showing this form dates from about 300 A.D. How much longer asses survived among the Atlas ridges is impossible to know.

Today, the closest known wild ass habitat to that of the Atlas subspecies is probably the massif country of Ahaggar and Tibesti in the Sahara (see map). Interestingly, the specimens that Tristram (in Harper, 1945) describes agree in coloration with the Nubian subspecies rather than with the Atlas form. Remembering Herodotus' record of wild asses west of the Nile, these Saharan populations may represent relicts of a wider distribution which neared that of the Atlas subspecies. Trans-Saharan distributions of other ungulates such as the addax and the scimitar-horned oryx support such a possibility. Some authorities argue that those Saharan asses are feral (Sidney, 1965). Part of the problem appears to be dilution from crosses with wandering domestic asses.

Owen (in Survival, 1972) gives dilution as the primary cause of the Nubian wild ass's disappearance from its stronghold on the plains along the Atbara River. Aggravating the problem of strayed domestic stock is the local practice of tying an estrous jenny at an isolated spot in hopes that a wild jack will serve her. Sometimes these females are abducted. Common to the regions inhabited by the Somali wild ass as well as the Nubian subspecies, wild crosses tend to yield hardier, larger, more active offspring. This same incentive encouraged vigorous capture efforts in the Red Sea coastal district; shipped to Arabia, the wild asses found a ready market as breeding stock (Harper, 1945).

Due in large measure to their ability to survive in the Danakil Depression, an extreme desert whose Afar tribesmen are just as extreme in defense of their crucial resources, the Somali subspecies hangs on at a population level probably somewhat exceeding 2,000 individuals, in contrast to its northern neighbor, which is extinct or nearly so (Survival, 1976). The Ethiopian highlands separate somaliensis from africanus where the rugged terrain runs close to the coast at the Gulf of Zula near Massawa (De Beaux in Harper, 1945). The two asses designated Asinus a. dianae as well as those forming the basis of Baron von Heuglin's E. taeniopus are generally viewed as the results of infiltration across the Massawa separation or of crossing with domestic stock (Harper, 1945; Groves, 1974; Willoughby, 1974). Reminiscent of the Atlas wild ass, they exhibit both shoulder stripe and leg bands. The *dianae* specimens were shot at Hafta Wadi, not far north of the highlands barrier. Von Heuglin made his sightings in this general area as well as at the ruins of Wadi Safra and on the Atbara River (Sidney, 1965). To the south of the barrier, especially in Eritrea which includes the separation zone, particularly small, dark asses with both shoulder and leg marks are occasionally reported in *somaliensis* herds; these individuals have also been referred to as *taeniopus*, but they are probably progeny of crosses with domestic donkeys (Groves, 1974).

Northern overlap zones

In northeastern Africa, the most recent distributional area of the vanished or vanishing Nubian wild ass was concentrated in the Sudan from the fifth cataract of the Nile to the area of Sennar and from the Nile with its tributary the Blue Nile toward the Red Sea coast. Proceeding southward, the Somali wild ass inhabits Eritrea, the Danakil, French Somaliland, and the Guban in northern Somalia. Seasonal migrations extend its range from northern Somalia into Ogaden (Groves, 1974) going as far south as the Webi Shebeli River of Ethiopia and the Somali border country (Lydekker in Harper, 1945; Sidney, 1965).

It is these movements from the Nogal Valley of northern Somalia south into Ogaden that bring wild asses into zebra country. For instance, both the Somali wild ass and Grevy's zebra (*E. grevyi*) have been reported--at different times--at Ime on the Webi Shebeli. The Somali wild ass and Grevy's zebra come within 100 km of meeting again on the other side of the mountains forming the eastern wall of the Great Rift. While Grevy's zebra penetrates the neck of the Great Rift Valley northward all the way to Awash National Park, the wild ass extends southward to Lake Hertale where the Rift Valley fans out into the Afar Triangle, which includes the Danakil (Survival, 1972).

Encouraged by the low chain of rift lakes from Lake Chomo to Lake Zwai and from there by the Awash River, the narrow neck of the Rift as it approaches the Danakil supports savanna and brush woodlands whereas the Ogaden side of the mountains is semi-desert acacia country. Thus, the Ogaden area is better suited for southward incursions by the desert-adapted asses, and this is where overlap occurs. On the other hand, the northern subspecies of the grassland Burchell's zebra group (*E. burchelli bohmi*) join Grevy's zebra only over the southern portion of their plateau brush habitat, but use the savanna neck as far north as Lake Zwai (Roosevelt and Heller, 1915).

Grevy's zebra, *Equus grevyi*

Grevy's zebra, largest and most northern of all the living zebras, retains fairly stable southern limits in Kenya even though it has declined markedly in Ethiopia and Somaliland (Sidney, 1965). Following the east bank of the Omo River, it extends into Kenya along the eastern shore of Lake Rudolf (Lake Turkana on new maps) which is more moderate than the baked and blasted western shore. Through the Marsabit National

Reserve it reaches the northern slopes of Mount Kenya (Sidney, 1965; Western, 1978). Then it follows the Tana River's northern bank past the level of the Lorian Swamp, but stops well short of the coast. From these limits north and east, Grevy's zebra inhabits the dry brushlands of Kenya's Northern Frontier District.

Apprehensive of the species' future, 1977 efforts of "Operation Zebra" moved 50 Grevy's zebras some 480 km south of their native range to the western sector of Tsavo National Park (Reader, 1979). The furor stirred by the drastic tactics has incited more efficient information synthesis showing that Grevy's situation is not so desperate as supposed, but that the rate of decline has been drastic (Rainy, 1978).

Among reports mustered by this sudden spotlight on Grevy's zebra is ". . . a hint of a substantial population in the South Eastern Sudan." (Rainy, 1978). Corroboration is needed. Although the locality varies--Kenya's Turkana country, northeastern Uganda--there are recurring rumors of Grevy's zebras west of Lake Rudolf. In the absence of convincing evidence, the possibility of confusion with the northernmost representative of the Burchell's zebra group, which definitely does occur west of Lake Rudolf, must be considered. Interestingly, the 10th century Arab historian El Masudi, who describes a striped equid inhabiting a region which appears to be west of the Nile, mentions the animals' small size (Ridgeway, 1905). This would fit a burchelline zebra better than Grevy's.

Grevy's zebras inhabit dry scrublands of rocky brush country and low plateaus. Typically, they utilize open brush areas. The Ethiopian highlands with their colder, wetter climate; the open plains of the Haud (in Ethiopia on the northern border with Somaliland); and the 150 km strip of coastal forest all limit the species. Within its habitat, human disturbance encourages increased brush use (Cobb, 1978). Akeley (1930) describes Grevy's habitat as follows. The brush is predominantly thorny. Acacias dot the landscape, and palms also grow near water. When the shallow pans dry up, wildlife concentrates near rivers. Waterholes are commonly 30 to 100 km apart, and ground water tends to be alkaline. There is almost always a breeze. After a crisp morning, the heat sets in from 0900 to 1000 hr and increases until 1400 hr. About 1500 hr the wind increases, bringing relief. Evenings are clear and refreshing.

In keeping with the low forage quality of their habitat, Grevy's zebras are adapted for energy conservation. Their particularly long heads have higher-crowned, more complex grinding teeth than other zebras (Willoughby, 1974). The grass of Grevy's pastures is often dry, and dust or grit increases its abrasiveness. Even Grevy's temperament shows adjustment. Compared to its smaller grassland relatives of the Burchell's group, Grevy's zebras generally interact less often and less energetically, maintain only minimal social bonds--mother-offspring--rather than keeping stable family groups, and tolerate bachelor males within territories (Rainy, 1978), as long as there is no interference with an estrous female. All these strategies conserve energy. Small group sizes, together with opportunistic movements of females while they are lactating and young while they are growing, promote efficient use of patchy resources. This efficiency is increased by the fact that territorial males stay off the resource unless conditions become extreme (Rainy, 1978).

Burchell's zebra group, Equus burchelli

The Burchell's zebras have the largest distribution of any African equid species (striped areas on map). Cabrera (1936) took the multitude of proposed subspecies that had accumulated during sporadic exploration by European naturalists and grouped them into four subspecies on the basis of coat pattern and locality correlations. It must be remembered, however, that each local variation grades into the next and that individual variation within herds could mark one individual with one subspecific name and another with a different designation, if locality were not taken into account. Also, modern relocation and restocking efforts bring a new source of gene flow.

Following Cabrera's scheme, E. b. bohmi (Grant's zebra, Bohm's zebra, etc.) extends south from its overlap with Grevy's zebra to the Ruvuma River and the upper tributaries of the Zambesi system. E. b. selousii (Selous' zebra) lives between the Ruvuma and the Limpopo. E. b. antiquorum (Chapman's zebra, Damaraland zebra, etc.) bridges the southern continent, stopping at the Kalahari Desert and the vicinity of the Vaal River. Next came the typical variety E. b. burchellii (Burchell's zebra in the strict sense) which extended from the Kalahari fringes to the Drakensberg and from antiquorum's limit to the Orange River. E. b. burchellii became extinct in about 1910.

A quick comparison with the vegetation map shows the common bond: grassland. The burchelline zebras favor grassland, either open plains or wooded areas with grass in the understory. Themida triandra, an abundant grass species found to be highly palatable for E. b. bohmi in East Africa (Gogan, 1973), is also a staple in the diet of other grassland animals such as wildebeest and topi (Talbot, 1964). Themida triandra flourishes as far south as E. b. burchelli's former domain, but there both Themida grassland and Burchell's zebra haunts end together.

Quagga, Equus quagga

Without anyone realizing until the process was nearly complete, another equid, the quagga, also vanished from Africa. As settlement pushed inland from the Cape, there had always been more quaggas in the new lands to the north. Progressive depletion raised little comment. However, the process halted at the Vaal River. Belatedly, people recognized there were no more quaggas. The last known individual was a mare in the Amsterdam zoo who died August 12, 1883.

Plotting the places mentioned in connection with quagga sightings and comparing the maximum limits with vegetation patterns reveals a clear correlation (Cary, 1970). The quagga's distributional area matches South Africa's distinctive karroo plains plus the area between the Orange and the Vaal Rivers, where karroo species intergrade with grassland species. As aridity increases westward, desert species characteristic of the Namib coastal zone intergrade with karroo species.

"Karroo" is a Hottentot word meaning "a dry place" (Brown and Brown, 1896). In this great expanse of inland plateau, the stony ground stretches before the observer with only the occasional kopje (hill) rising out of the plain. Flat, dry, and almost treeless, the ground has a monotonous cover of xeromorphic plants. These are mainly low shrubs and succulents with a few grasses. The plants tend to grow in widely spaced clumps, each clump being an association of three or four species rather than a single species (Hutchinson, 1946). Leslie Brown (1965) characterizes the karroo as ". . . a multitude of bushes, each growing in its own little desert." Many succulents shelter by these spiny bushes. Nights are cold; days are clear and hot. The daily temperature range on the Great Karroo is about 48°C (Brown and Brown, 1896). Rainfall varies from about five to fifteen inches annually with more falling in the east than in the west. Most of the rain comes during April to August in the form of heavy thunderstorms which send torrents of water dashing down the gulleys. Most of the streams are periodic. Acacia karroo often grows along watercourses (Palmer and Pitman, 1961).

Along the southern coast, running roughly between the Orange River and the Oliphants River, is the Succulent Karroo for which grasses are common in its eastern section (Hutchinson, 1946; Keay, 1959). Here, as on the Little Karroo in which the vegetation is transitional between that of the larger karroo plateaus to the north and the Cape macchia to the south, the genus Mesembryanthemum is prominent (Keay, 1959; Brown, 1965). The family Papilionaceae is characteristic of the karroo in general and also of the macchia (Hutchinson, 1946).

Mountain zebra, Equus zebra

The mountains near South Africa's most southern coast gave early European settlers their first look at zebras. These small Cape mountain zebras, E. z. zebra, inhabit plant associations with more elements of Cape macchia of the coastal plateau than of the karroo. The Cape macchia consists principally of several shrub layers (Brown, 1965). These shrubs are generally evergreens with stiff, leathery leaves. Shrubs containing oil or resin are common (Keay, 1959). Trees are rare. Although there are only occasional patches of grass, reedlike Restionaceae abounds (Hutchinson, 1946). Where not disturbed by man, the macchia stretches from the sea coast to the tops of the first mountain ranges (Brown, 1965).

Hartmann's mountain zebras, E. z. hartmannae, utilize lightly vegetated parts of the Namib Desert. Their habitat stretches along the southwestern coast of Africa from south of the Great Fish River to well north of the Cunene River. "Namib" is the Hottentot word for "desert." Unlike the Kalahari to its east, the Namib has very little plant cover, in large sections none. Although not as hot as the Sahara, the Namib is extremely arid. Huge, red dunes run in seemingly endless procession along the coast. The vast plains and deep gorges are strewn with rocks. Inland, the summer winds sometimes bring five to eight centimeters of rain all dropped during a violent cloudburst (Martin, 1960). Then a few flowers may appear by the drying watercourses and, overnight, ephemeral grasses spring up attracting large concentrations of the highly migratory game (Martin, 1960). This uncertain rainfall means a shifting line between desert and semi-desert. "Heavy" rains bring grazing that may last up to two years, but such a rainy season may only come once every eight years (Martin, 1960). The rest of the time there is only the nightly fog which rolls in from the sea. The scraggly baobab trees store water in their trunks. The aloes and euphorbias with their poisonous sap and the few small bushes with their spines offer little to the hoofed inhabitants. Conveniently, Hartmann's zebras are specialists in locating water. They can dig through a meter of sand and gravel in a dry stream bed to reach it (Martin, 1960).

Southern overlap zones

E. b. antiquorum of the Burchell's group overlaps Hartmann's zebra north of the Kalihari where grassland meets the narrow portion of the desert strip along the coast. The two species actually use some areas such as waterholes at the same time, but they show no special affinity for each other (Klingel, 1968).

The quagga showed two different kinds of overlap. Its native karroo surrounds pockets of mountain zebra habitat in the south but gradually transforms into grassland in the north. In the south, ecological isolation was distinct. Quaggas kept to the inland plains, only coming within sight of mountain zebras occasionally if a troop came down from its mountain stronghold in search of water or salt. Fig. 3 shows the alternating character of their habitats by diagramming the interspersion of mountain ranges and plains. Since the mountains are not uniform in height or extent, quaggas could wander from one plateau to another. Passing from the Orange River to the Vaal River, karroo plant species decrease as grassland species increase. There are no spectacular topographic variations as in the south. The typical form of the Burchell's zebra used this region alongside the quagga. However, each still kept to its own herds (Harris, 1969). In addition, each regularly herded with a different species of gnu: the quagga with the white-tailed gnu (Connochaetes gnu) and the Burchell's zebra with the brindled gnu (C. taurinus) (Harris, 1969). These two gnus show a similar overlap pattern in their northern and southern limits, respectively, to that of their equine associates (Harris, 1969; Von Richter, 1971).

Despite the individual variation in coat pattern evident within both quagga herds (Daniell in Pocock, 1904) and Burchell's zebra herds (Buckley, 1876; Stevenson-Hamilton, 1912), local observers easily distinguished two different animals within the same region (Harris, 1852, 1969). This, in combination with the vegetation correlation, indicates a higher order of separation than the subspecies level. Although necessarily dealing with small sample sizes, skull measurements studied by Hilzheimer (1912), Cooke (1943), and Lundholm (1951) support a distinction at the species level. Especially now that extinction has withdrawn the quagga from any further evolutionary role and has also removed its closest link with the Burchell's group, the typical Burchell's zebra, the vegetation and other indicated differences seem enough to justify retaining both the names Equus quagga (for the extinct quagga) and Equus burchelli (for the Burchell's group).

Conclusions

When mapping the areas inhabited by species of the genus Equus in Africa, it is impossible to display for all species maximum limits before decline due to man's activities. The Atlas wild ass disappeared in Roman times, and what appear to be relict populations of the Nubian wild ass in the Sahara suggest a former chain of massif populations reaching westward across the Nile toward the Atlas mountains. The distinction between changes due to human influences and evolutionary changes--for example, increasing the effects of aridity in the Sahara--becomes unclear. Even excluding the wild asses, one would have to pick a date earlier than the European discovery of some of the forms. The quagga became extinct the year after the last of the zebra species was originally described. Thus, any map like Fig. 1 is a composite.

Because of inevitable shrinkage of available range caused by changing land use practices and human population increase, it furthers our understanding of a genus such as Equus to have a well formulated idea of former distribution. This paper attempts to formulate such a baseline. Much detailed information is still needed, especially from the Sudan, but the present results are still instructive. When published data is rendered in map form, it clarifies our thinking and requires further revisions to be precise. Including the African wild ass along with all the zebra species helps remind us to look beyond categories based only on one characteristic, such as color, and to examine large units of the genus with a more open perspective.

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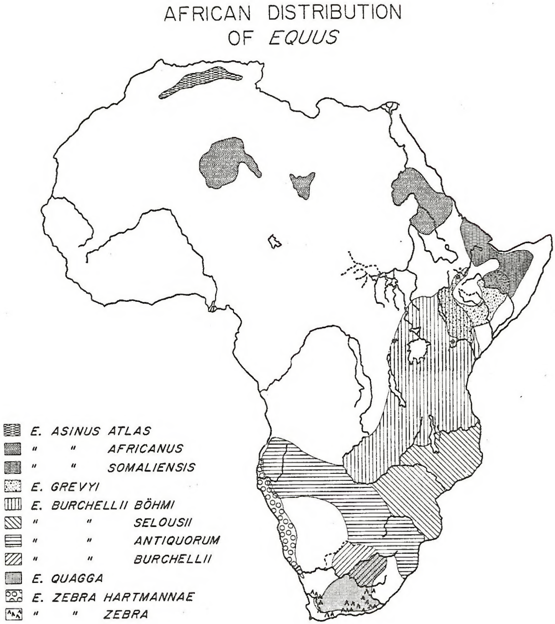
AFRICAN DISTRIBUTION OF *EQUUS*
E. ASINUS ATLAS
" " AFRICANUS
" " SOMALIENSIS
E. GREVYI
E. BURCHELLII BÖHMI
" " SELOUSII
" " ANTIQUORUM
" " BURCHELLII
E. QUAGGA
E. ZEBRA HARTMANNAE
" " ZEBRA

Figure 1. African distribution of the genus Equus showing maximum historical limits. Principal sources used: E. asinus--Harper, 1945, and Sidney, 1965; E. grevyi--Roosevelt and Heller, 1915; E. burchelli--Shortridge, 1934, and Cabrera, 1936; E. quagga--Cary, 1970; E. zebra--Shortridge, 1934, and Harper, 1945.

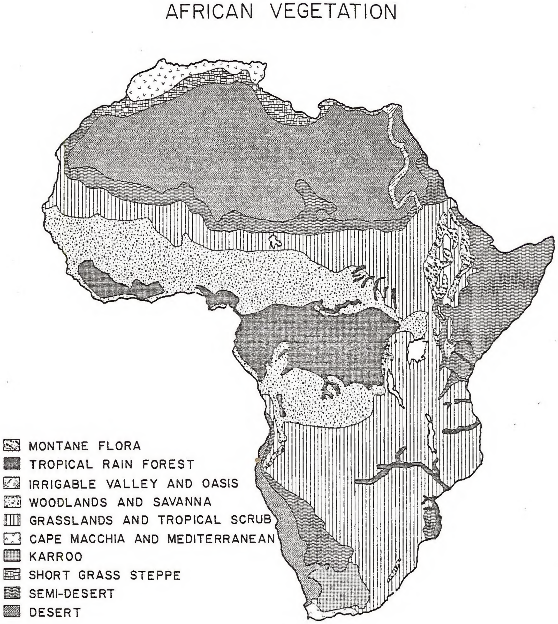
AFRICAN VEGETATION
MONTANE FLORA
TROPICAL RAIN FOREST
IRRIGABLE VALLEY AND OASIS
WOODLANDS AND SAVANNA
GRASSLANDS AND TROPICAL SCRUB
CAPE MACCHIA AND MEDITERRANEAN
KARROO
SHORT GRASS STEPPE
SEMI-DESERT
DESERT

Figure 2. African vegetation zones. Principal sources used: Bartholomew, 1958, and Keay, 1959.

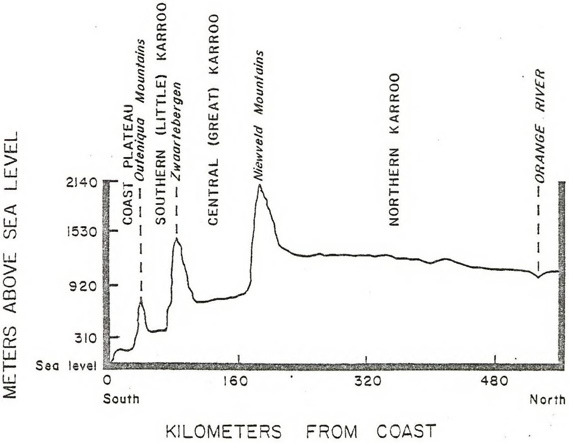

Figure 3. Topographic profile showing interspersions of mountains and karroo plateaus in southern Africa. Cross section from Knysna through Beaufort West, adapted from Brown and Brown, 1896.

Feral Horse Demography: A Preliminary Report

Michael L. Wolfe
Department of Wildlife Science, Utah State University, Logan

Abstract

The demographic characteristics of 18 feral horse (*Equus caballus*) populations in five states are discussed. As estimated primarily from the results of composition counts, foals comprised an average 19 percent (post-parturition) of the population analyzed. Various procedures were employed in an attempt to estimate survival rates within the populations. Provisional estimates of first-year survival rates span the general range of 50-70 percent, while those for adults may approximate 80-85 percent. Annual rates of increase, predicted from simulation runs with the estimated population parameters, were considerably lower than those "observed" from aerial inventories in successive years. Possible explanations for these discrepancies and management implications are discussed.

Population Dynamics of Feral Ponies

Ronald R. Keiper
The Pennsylvania State University, Mont Alto

Abstract

Since 1975 data have been collected on the population dynamics of the feral ponies that inhabit Assateague Island, a 37-mile barrier island along the Atlantic coast of Maryland and Virginia. Foalings occur from April to September, with about 50% of all births taking place during the month of May. About 70% of all mares three years of age and older bear a foal each year. There has been no record of a mare less than three years old foaling, and no multiple births have been observed during the study period.

The sex ratio of the foals varies widely from year to year but seems to average out at the expected one male:one female ratio.

Compared to natality, the mortality rate among the Assateague ponies is less than 10%, and many of these deaths have resulted from actions of man. Most deaths occurred in late summer or in late winter. Diseases like equine infectious anemia and equine encephalitis also act to control the size of the population.

Introduction

Feral ponies have lived on Assateague Island, a 37-mile-long barrier island along the Atlantic coast of Maryland and Virginia,since at least the mid-1600's. The ponies roam freely about the island and obtain their own food and water throughout the year.

Presently about 180 ponies are found on Assateague. These include approximately 60 animals inhabiting the northern (Maryland) portion of the island and 120 ponies occupying the Chincoteague National Wildlife Refuge on the southern (Virginia) end of the island. The Maryland ponies are owned by the National Park Service and live within the Assateague Island National Seashore. The National Park Service views these feral animals as part of the native fauna and does not manage them in any way at the present time.

The ponies living on the southern portion of Assateague are owned by the Chincoteague, Virginia,Volunteer Fire Company. These animals are rounded up each year during the last week in July and most of the foals are sold at auction. In addition, adult ponies are moved from band to band or removed from or added to the island by their fireman owners.

Since 1975, data have been collected on the population dynamics of both groups of ponies. This paper presents some of this information.

Methods

Because the ponies were acclimated to the presence of man, they could be observed from distances of about 5 meters without affecting their normal behavior. All of the ponies in the study area could be recognized individually by differences in color, size, sex, and markings. An identification sheet was completed for each animal, containing the pertinent data for recognition, and a color photograph was taken and filed for future reference. Because of this individual recognition, each pony could be followed through time and pertinent data could be collected on it.

Results and Discussion

Sex and Age Characteristics

Because of the manipulation of the ponies on the Virginia portion of Assateague Island, the data on sex and age presented in Table 1 apply only to the Maryland ponies. The uneven sex ratios seen in adult (1 male: 2.12 females) and immature animals (1 male:3.08 females) differ from the results obtained by Feist and McCullough (1975) and probably result from different dispersal patterns between the sexes, emigration of young males out of the study area, and the longer period of study. The sex ratio in the younger age classes is closer to the expected 1 male:1 female because dispersal has not yet occurred in these groups.

There are also differences in the age structure of the Assateague ponies compared to the Pryor Mountain horses. Feist and McCullough (1975) found more mature animals (58.1% of the population) and fewer immature animals (17.8%) than the present study, but they admit difficulty in distinguishing immature horses, whereas most of the Assateague ponies are of known ages. Other differences between the two studies result from a lower frequency of foaling among Pryor Mountain mares and a higher mortality of animals during their first winter.

Seasonal Distribution of Foaling

Unlike zebra, which have no great marked season of birth and foal throughout the year (Klingel, 1969), horses and ponies do show a definite birth period. Tyler (1972) found that 96% of 294 births recorded in the New Forest ponies occurred in April, May, or June. Three percent of all foalings took place in March and July, and only 1.3% occurred in August and September. No births were recorded at other times of the year.

Table 2 presents the seasonal distribution of 142 foalings for ponies living on both the Maryland and Virginia sections of Assateague. Young were born only from April to September, with almost half the births (47.18%) occurring in May. Compared to Tyler's results, the Assateague ponies showed a lower percentage of births in April, May, and June (only 83.10%) and more births in July, August, and September (16.90% compared to Tyler's less than 4%).

Sex Ratio of Foals

Although the sex ratio of the foals born on Assateague varied from year to year, over the five years of the study there was no significant difference in the total number of colts and fillies (Table 3). Klingel (1965) found a sex ratio of 85 males to 100 females in zebra over a two-year period, while Feist and McCullough reported that 19 colts were born in 1970 to 16 fillies in the Pryor Mountain horses. Tyler (1972) found no significant difference in the sex ratio of foals born in New Forest in 1966 and 1968, although in 1967 there were 1.7 female foals born for each male foal. For the three years of study, the sex ratio was 45.55% male to 54.45% female.

Foaling Rate

Although Hammond (1960) quoted a figure of 95% fertility for pony mares running with stallions, this figure is too high for the Assateague ponies. The five-year results presented in Table 4 show that within the Assateague Island National Seashore, the percentage of mares that foaled each year varied from 43.5% in 1979 to 70.5% in 1977. The five-year average was 61.4%. The foaling rate for mares living within the Chincoteague National Wildlife Refuge varied from 81.0% in 1976 to 70.83% in 1979, for a four-year average of 74.4%. This higher foaling rate may result from the fact that the Virginia mares, which do not have to nurse the previous summer's foal through the winter, suffer a lower rate of abortion. A mare who was still nursing a yearling on the Maryland portion was observed to abort a young fetus in September 1978. Tyler (1972) noted that abortions were common in New Forest pony mares in late autumn, winter, and early spring and contributed to a low foaling rate.

The foaling rate recorded for the Assateague ponies is somewhat higher than that found by other workers. Feist and McCullough noted that only about 50% of the Pryor Mountain mares gave birth to a foal in 1970. Tyler presented a three-year foaling rate of 46% for the New Forest ponies. In that study, however, the number of stallions was restricted by man, and it is possible this factor helped lower the foaling rate.

Foaling Frequency

In addition to determining the foaling rate, 49 mares who were three years old or more in 1975 were followed over a four-year period to determine the frequency of foaling. The foaling frequency for these mares is presented in Table 5. Most of the mares (36.74%) gave birth to three foals over the four-year period, although 18.37% of the mares did foal each year. Only three animals (6.12%) failed to foal at all during the period.

Tyler (1972) reported that few of her mares foaled each year during the three-year study, and said it was common for a mare to foal in alternate years. (Foaling in alternate years was rather rare in the present study, occurring in only 10.20% of the mares). Klingel (1969) followed 120 plains zebra mares for three foaling seasons, and found that only 15% of them had three foals, 33% had two, 42% had one, and 10% produced no offspring. Since these data represent surviving foals, and since these animals suffer a higher mortality rate than Assateague ponies, the differences between the two populations are easily explained.

Age at First Foaling

Although Tyler (1972) noted that some of her mares came into estrus as yearlings and one mare foaled at two years of age, this does not seem to be the case on Assateague Island. Mares come into estrus during their second summer, and some mares produce a foal when three years old. However, this number may be rather low, for of eight mares known to be three years old, only three produced foals. Feist and McCullough (1975) also recorded that a few three-year-old mares foaled during that study.

Twinnings

No twins were born during the study. According to Tyler (1972), who failed to observe any twins during her three years of observation, twinning is rare in equids, and if twins are conceived, they generally are aborted at an early stage. Klingel (1969) also failed to observe any twin births in the plains zebra, but Feist and McCullough (1975) reported two sets of identical twins present in the Pryor Mountain population.

Mortality in Foals

During the study, seven foals were known to have died, although additional foals may have been born dead or died shortly after birth without being recorded. Six of the foals died within the first three days of life. One had been stepped on by another pony and suffered a broken leg and internal injuries. It died several hours after the incident. Two other foals showed no interest in nursing and suffered from diarrhea before they died. The causes of death of the other young foals were unknown. The foals were observed on their first day, then never seen again.

The death of foals after their first few days was unusual; only one such death occurred during the course of the study. This animal, a ten-week-old foal, died after it failed to find its mother following a separation of several days. The death occurred in August when the foal was subjected to blood loss by abundant, blood-sucking horseflies.

Tyler (1972) reported that nine foals died, during her three-year study, as the result of premature births, weakness, accidents, and rejection of foals by their mothers. In addition, 18 other foals were killed or had to be destroyed as the result of road accidents.

Mortality in Older Ponies

During the period June 1975 to June 1979, only 11 ponies over one year of age were definitely known to have died on the Maryland portion of Assateague. These deaths represent a mortality rate of less than 10%. Only six of the deaths resulted from natural causes. All but one of these animals were over ten years of age and died between November and April. The other animal was a two-year-old female that died in September 1978 of bloodworm infestation. The five other deaths resulted from road accidents or attempts by Park Service personnel to tranquilize the animals.

Although a mortality rate cannot be calculated for ponies living on the Virginia portion of Assateague, because of periodic removals carried out by the owners of these animals, 12 deaths have been documented. Two old males, both over 20 years of age, perished during the winters of 1976 and 1977, and examination of their skulls revealed that the lower incisors were completely gone and the grinding teeth badly worn. Six ponies, including four animals one to three years old, died in a short period from August 26-September 7, 1975. Symptoms resembled equine encephalitis, and that disease was subsequently detected among the human population in the nearby town of Chincoteague, Virginia. Equine infectious anemia has also been documented in the Virginia ponies, and may have resulted in the death of two ponies. Finally, a two-year-old female suffering from a badly infected leg disappeared in November 1976 and has not been observed since.

Tyler (1972) reported that 13 ponies older than one year were killed in road accidents during the period 1966-68, and that an additional 27 other ponies died from a variety of causes. These included poisoning, poor nutrition resulting from teething problems, and problems during foaling. A number of other animals suffering from poor nutrition were removed from the New Forest before death occurred. Approximately 65% of the deaths resulting from poor nutrition affected ponies older than 12 years, and all such deaths occurred between November and April.

Conclusions

The data on the population dynamics of the feral ponies living within the Assateague Island National Seashore, collected since 1975, show that the size of the population is increasing. Annual reproduction averages about 20%, while annual mortality averages less than 10%. Growth of the population has been slowed by emigration out of the area and by deaths resulting from human actions. Since preliminary data on the carrying capacity suggest a maximum population of 100-150 animals, management policies and procedures concerning control of the size of the population should be initiated.

Population growth on the southern part of Assateague, within the Chincoteague National Wildlife Refuge, has been controlled by the annual removal of 25-40 foals. However, studies should be undertaken to determine the effect of the 150 ponies, permitted to graze there under federal permit, on the ecosystem.

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Table 1. Age Structure of the Population of Assateague Island Ponies, 1975-1979.

in Age Class

	Mature	Immature	Yearling	Foal	Total	%
# Male	31	24	24	22	101	32.06
# Female	85	74	25	30	214	67.94
Total #	116	98	49	52	315	
As % of Total Population	36.83	31.10	15.56	16.51		

Note: Immature animals were ponies two and three years old. All foals were from mature females except three born to three-year-old females.

Table 2. Seasonal Distribution of Foaling in the Assateague Island Feral Ponies

Month	# Foals Born
April	24
May	67
June	27
July	15
August	5
September	4
	142

Table 3. Sex Ratio of Assateague Pony Foals

Year	# Males		# Females
1975	41	:	20
1976	19	:	21
1977	14	:	23
1978	15	:	10
1979	11	:	16
TOTAL	100	:	90

Table 4. Foaling Rate of Mares in Assateague Island Feral Ponies

	% of Mare Foaling	
Year	AINS	CNWR
1975	58.8% (10/17)	70.9% (27/38)
1976	64.3% (9/14)	81.0% (30/37)
1977	70.5% (12/17)	75.0% (28/37)
1978	70.0% (14/20)	---
1979	43.5% (10/23)	70.8% (17/24)
Five Year Average	61.4%	74.4%

AINS = Assateague Island National Seashore

CNWR = Chincoteague National Wildlife Refuge

Table 5. Frequency of Foaling for Assateague Island Feral Pony Mares, 1975-1978.

	# Years in Which Mare Produced a Foal				
	4 yrs.	3 yrs.	2 yrs.	1 yr.	0 yrs.
# Mares Foaling	9	18	14	5	3
%	18.37%	36.74%	28.57%	10.20%	6.12%

Note: For those mares that produced two foals in the four years, nine mares (18.37%) had foals for two consecutive years, while five mares (10.20%) had a foal every other year.

The Mare-Foal Demography of Feral Horses in Wyoming's Red Desert

Lee Boyd
Department of Zoology and Physiology, University of Wyoming, Laramie

Abstract

Ground observations and flights were used to study the 1978 and 1979 natality and foal survivorship of feral horses in Wyoming's Red Desert. The 1978 natality was 29.5 foals per 100 other horses (n=373 horses). In contrast, 1979 natality was only 21.7 foals per 100 other horses (n=398 horses). Approximately 78% of the mares aged three or older foaled in 1978. Only 53% of the mares aged three or older foaled in 1979. In 1978 survivorship to one month of life was 86%; 82% lived to two months of age, and all of these survived to yearling status (n=51). In 1979 survivorship to one month of age was 100%, and 98% survived to two months of age (n=43). The 1979 survival to yearling status is not yet known. The difference between the parameters in the two years reflects the difference in the winters. The winter preceding the 1978 foaling season was mild; the winter preceding the 1979 season was relatively severe. Several theories are proposed as explanations of the winters' effects on these parameters. Most foals are born from late March through August with a peak in May and June. The sexes of the foals closely approximate a 1 to 1 ratio. Mortality is highest in the first week of life. Sources of mortality are discussed and management implications are also given.

Introduction

A knowledge of mare-foal demography is important in determining equid population trends and in developing management practices. Although many equid studies mention natality and foal survivorship, few do so in depth and most of these populations have not been located in areas scheduled for intense management. This study is one of the first to deal specifically with mare-foal demography in a population which is to be controlled by the Bureau of Land Management, and the data gathered are of special interest in light of the controversy over BLM's management of feral horses in the West.

Several authors have examined the effect of weather on equid demography. Klingel (1969) found the productivity of plains zebra (Equus quagga) to be correlated with rainfall, and Welsh (1975) discovered that the number of feral horses born on Sable Island each year was related to the severity of the preceding winter. This study relates two years of natality and foal survivorship data to the severity of the winter preceding each foaling season. Length of the foaling season, foal sex ratios, and foal mortality are also reported.

Study Area

The study area is located approximately 48 km northeast of Rock Springs, Wyoming. The 746 km^2 site is part of the Red Desert and is a sagebrush grassland community with an average annual precipitation of 22.33 cm (U.S. Dept. of Commerce, 1977, 1978). During the early spring many temporary water holes are created by snow melt and occasional rain showers, but from late spring into the fall, a few artesian wells are the only available water sources.

As many as 700 horses may be present on the site during the summer when animals congregate near available water sources (Richard Miller, Dept. of Zoology and Physiology, University of Wyoming, Laramie; pers. comm.). This horse population has been studied extensively since 1976 by Richard Miller and Dr. R. H. Denniston (Miller and Denniston 1977, 1979; Denniston and Miller, 1978; Denniston, 1979; and Miller, 1979, 1980). My own research on this population began in 1978.

Methods and Materials

The study ran from 1978 through 1979. Bands were located and observed using 7 X 50 binoculars and a 20X spotting scope. Observations were handwritten in field notebooks.

Each band was given a letter designation. Many bands already identified by Richard Miller were also used in this study, and his photo file of these bands was of great help in their identification. Individual members of each band were identified by their color and markings and were aged whenever possible. Year of birth was known for some of the younger horses. Yearlings and two-year-olds could also be aged on body size and tail length relative to the adults. Yearlings are considerably smaller than adults and their tail does not extend past the hock. Two-year-olds are larger than yearlings but still not as large or as well-muscled as adults. Their tail extends only halfway down the cannon bone whereas the tail of the adult extends to the fetlock. Older horses could be classified only as "adults" and were impossible to age in the field. A few very old animals could be classified as "aged" based on subjective observations of their general appearance, loss of muscle tone, and behavior. Each individual was listed by band affiliation in a card file system.

Bands were located and observed as often as possible throughout 1978 and 1979 in order to note band composition. From these observations natality could be determined both in terms of foals per 100 other horses, and as the number of adult mares foaling. In calculating the 1979 natality, new bands identified after the 1978 foaling season were also included since t tests between bands identified in both years and new bands identified only in 1979 showed no significant difference at the 95% confidence level. The number of mares foaling each year, foaling dates, foal sex ratios, and foal survivorship and mortality were also noted. Most of the work was done from the ground, but flights over the area were conducted during the winters when the site was otherwise inaccessible.

Weekly ground counts of the number of foals per 100 other horses were made as frequently as possible during the main foaling season. Both known and unknown bands were used. A regression line was fitted through the data points for each year so that a comparison of the two years could be made (Sokal and Rohlf, 1969).

Natality and foal survivorship data from both years were compared by a series of t tests. The finite population correction factor was used in computing significance levels, since a substantial amount of the population was sampled (Mendenhall et al., 1971). This correction factor is not yet in common usage, so computing formulas and an example will be given here.

The finite population correction factor equals $1 - \frac{n}{N}$, where n is defined as the sample size, and N is the total population size. Comparisons were made by including the finite population correction factor into the formula for testing the difference between two proportions, $\hat{p}_1$ and $\hat{p}_2$. The test statistic, z, becomes

$$z = \frac{(\hat{p}_1 - \hat{p}_2)}{\sqrt{[\mathrm{var}(\hat{p}_1)+\mathrm{var}(\hat{p}_2)](1-\frac{n}{N})}} = \frac{(\hat{p}_1 - \hat{p}_2)}{\sqrt{\left[\frac{\hat{p}_1(1-\hat{p}_1)}{n_1} + \frac{\hat{p}_2(1-\hat{p}_2)}{n_2}\right](1-\frac{n}{N})}} .$$

In this study, data were collected on approximately 400 horses each year and a generous estimate of the total population size was 800 horses. Thus the finite population correction factor used in all of the t tests was $1 - \frac{400}{800} = .5$. This is a conservative number, and it is likely that the variances could be cut even more by using more concise estimates of population size in the denominator.

As an example computation, the comparison of 1978 and 1979 natalaties in terms of foals per 100 other horses would be calculated as follows. First, in order to have true proportions, the numbers would have to be converted back to foals per total horses rather than per 100 others.

$$\hat{p}_1 = 1978 \text{ natality} = \frac{29.5 \text{ foals}}{100 \text{ others} + 29.5 \text{ foals}} = \frac{29.5 \text{ foals}}{129.5 \text{ total horses}} = .228$$

$$\hat{p}_2 = 1979 \text{ natality} = \frac{21.7 \text{ foals}}{100 \text{ others} + 21.7 \text{ foals}} = \frac{21.7 \text{ foals}}{121.7 \text{ total horses}} = .178$$

$n_1 = 373$ horses

$n_2 = 398$ horses

$$\text{Thus } Z = \frac{.228 - .178}{\sqrt{\left[\frac{.228(.772)}{373} + \frac{.178(.822)}{398}\right](.5)}} = \frac{.05}{\sqrt{.0002364 + .0001838}} =$$

$$\frac{.05}{\sqrt{.00041975}} = \frac{.05}{.02048771} = 2.4405$$

This is significant at the 99% confidence level, hence $p < .01$. A 95% confidence interval on the difference in the two proportions is given by

$(\hat{p}_1 - \hat{p}_2) \pm Z(\sqrt{[\mathrm{var}(\hat{p}_1) + \mathrm{var}(\hat{p}_2)](1 - \frac{n}{N})})$ which in this case

becomes $.05 \pm 1.96(.02048771)$ or $.05 \pm .040$. Unfortunately, there is no known method that will convert this confidence interval on the difference back to an equivalent interval in terms of foals per 100 other horses (Dr. Lyman McDonald, Dept. of Zoology and Physiology, University of Wyoming; pers. comm.).

Results and Discussion

Weather

The winter preceding the 1978 foaling season was relatively mild. Average monthly temperatures were above normal and the snow melted before much could accumulate (Table 1).

In contrast, the winter preceding the 1979 foaling season was more severe and temperatures were often below normal. Nightly temperatures in late December and January frequently dropped below -10°C (Table 1). Wind chills down to -40°C were common. Much snow fell and the cold temperatures allowed it to accumulate and drift. Flights over the study site showed that some areas were blown free of snow, while in other areas horses stood up to their bellies in snow with their heads disappearing into the foraging craters they had pawed.

Natality and Survivorship

The two winters had differing effects on natality and foal survivorship. In 1978 after the mild winter, natality was 29.5 foals per 100 other horses with foals comprising 22.8% of the entire population. Approximately 78% of the mares aged three or older foaled, and 86% of the mares aged four or older foaled (Table 2). The 1979 natality was only 21.7 foals per 100 other horses with foals comprising 17.8% of the total population. Only 53% of the mares aged three or older foaled, and 54.5% of the mares aged four or older foaled. These are minimum estimates since some mares might have foaled and lost their offspring in the first few days of life before I was even aware of the birth.

Figure 1 compares natalities for the two years in terms of foals per 100 other horses throughout the main foaling season. The main foaling season is from late March through August with a peak in May and June; however, a few foals are born at other times of the year. Towards the end of the 1978 season deaths exceeded births. This was not apparent in 1979 because nearly all of the foals survived.

Foal survival for both years was high, but there was a significant difference between the two years (Table 2). Fifty-one foals born in 1978 were followed through their first year of life. Of these, 86.3% survived to one month, 82.4% survived to two months and then on to yearling status despite the ensuing harsh winter. Although fewer foals were born in 1979, nearly 100% survived. Forty-three of these foals were followed to two months of age. All survived their first month; 97.7% survived to two months. Survival to yearling status is not yet known.

Natality and foal survivorship data from both years were compared by t tests to prove that they were statistically different from one another. All comparisons were significant at the 95% confidence level (Table 2). A significant difference between the two years is shown by placing 95% confidence intervals on the natality lines in Figure 1.

Several factors might be responsible for the one-third reduction of natality in 1979. In some equid populations the mares foal in alternate years or every third year (Klingel, 1969; Tyler, 1972; Moehlman, 1974; Nelson, 1978). Examination of the two-year foaling record indicates that the Red Desert population is also on an alternate year cycle, as many mares foaled in 1978 but not in 1979. However, a small sample of long-term data from the population suggests otherwise. Complete records were available for eight mares first identified by Richard Miller in 1976. Of these, seven mares foaled in all four years, while the other one foaled in each of the first three years but not in 1979 after the harsh winter. Rather than an alternate year pattern this suggests consecutive foaling which was disrupted for one season by the severity of the winter.

A closer examination of the 1978 and 1979 data supports this hypothesis. Of 70 mares who were adult in 1978 and whose foaling record is known, 33 (47%) foaled in both years. Of the 37 who did not foal consecutively, 22 (60%) of these foaled in 1978 but not in 1979 after the severe winter. Conversely, only nine (24%) foaled in 1979 that had not also foaled in 1978 after the mild winter; a significant difference from the previous case at the 99.5% confidence level. Three of these nine were actually primiparous four-year-olds. Six (16%) of the 37 who did not foal consecutively actually foaled in neither year and at least half of these were nulliparous.

The mares were in excellent condition following the mild winter of 1977/1978, so there was no reason for them not to come into estrus. Since most had already foaled by June (Table 5) they could have cycled for at least five estrous periods before going into anovulation, and it is hard to believe that they would not have conceived. Fetal reabsorption is also an unlikely explanation for the reduction in natality, as Belonje and van Niekerk (1975) found that if a mare was kept on a reasonable plane of nutrition until 35 days after conception, food intake could then be reduced without reabsorption occurring. Since green-up in the Red Desert occurs just before and during the breeding season, and since most of the mares appeared to be in good condition in 1978, it is doubtful that many fetuses would have been reabsorbed.

More likely, most of the reduction in the 1979 natality was due not to lowered rates of conception or fetal reabsorption, but to abortions and stillbirths as a result of winter stress. Both Tyler (1972) and Welsh (1975) noticed winter-induced abortions in the feral horse populations they studied. Nishikawa and Hafez (1974) report that the average rate of abortions is high (10%) in domestic mares and that the mare is endocrinologically susceptible to abortions during the fifth and tenth month of pregnancy because of hormonal deficiencies. They suggest that it is best to avoid sudden changes in diet and exercise at this time. These susceptible periods coincide exactly with the 1978/1979 winter months when the mares would have been the most stressed physically and nutritionally. Hafez and Jainudeen (1974) state that mares may abort due to reduced energy intake. Others feel that the mares would have had to be in extremely poor condition before they would abort (Dr. Ed Squires, Animal Reproduction Laboratory, Colorado State University, Fort Collins; Dr. Jim Waggoner, Dept. of Animal Science, University of Wyoming, Laramie; pers. comm.). Since most of the Red Desert mares were not drastically underweight despite the severe winter, their foals were more likely carried to term but born weak or dead. Yeates and Parer (1959) state that undernutrition in ewes causes stillbirths. Live young born to undernourished sheep and cattle are usually underweight, die easily of exposure, and lack the inclination to suckle (Yeates and Parer, 1959; Rattray, 1977). In addition they state that poor nutrition lowers the dam's milk production and inhibits the maternal instinct. In the Red Desert the severe 1978/1979 winter conditions may have resulted in abortions, stillbirths, and weak foals which died soon after birth. This would have lowered the observed 1979 natality and perhaps weeded out the weaker fetuses so that those who survived their first day of life were the healthy ones likely to continue to survive. This would explain the high 1979 survival rate. Welsh (1973) surmised that something similar was occurring in the feral horse population on Sable Island. In 1971, 76% of his adult mares bore full-term foals but 25% of these foals died in the first week of life. In 1972 after a hard winter only 38% of the adult mares bore full-term foals and 13% died in the first week of life. The difference in birth rates was due to abortions at the end of a harsh winter.

Age-Specific Effects

Although several yearlings were bred, no mares younger than three years of age foaled during the entire study. Thus, three seems to be the minimum age of parturition, and these mares have a lower foaling rate than the older age classes. In each of the two years of this study, a third or less of the known three-year-olds foaled.

If three-year-olds are included in the 1978 natality estimates, the foaling rate is 8% lower than if only four-year-olds and older are considered. This is a significant difference at the 95% confidence level (Table 3). In 1979, including three-year-olds only lowers the rate by 2%, which is not significant. More three-year-olds might have foaled in 1979 after the severe winter than in 1978 after the mild one. This would seem unlikely, since the older mares were doing exactly the opposite, but it is supported in that one out of nine known three-year-olds foaled in 1978, while four out of 12 foaled in 1979. Nothing in the literature suggests a reason why more three-year-olds should foal after a bad winter than a good one, and perhaps this "trend" is merely an artifact of the small sample sizes. If so, another possibility is that the number of young mares foaling might have remained nearly constant in both years. However, the proportion of older mares foaling may have dropped in 1979, if they were more affected by the harsh winter than the younger females. Reducing the ratio of older females with foals to younger females with foals would also tend to equalize the foaling rates with and without three-year-olds seen in 1979.

Several researchers agree that older mares are more likely to be adversely affected by prolonged rough weather than younger mares (Dr. Terry Nett, Dept. of Physiology and Piophysics, Colorado State University, Fort Collins; Dr. Ed Squires, Animal Reproduction Laboratory, Colorado State University, Fort Collins; Dr. David Yates, Department of Animal Science, University of Wyoming, Laramie; pers. comm.). The older females would be stressed by several years of constant pregnancy and lactation, while three-year-olds would never have lactated and would be pregnant for the first time only. Thus older mares might be more likely to lose their foals in a bad winter, while younger mares would be less stressed and their foaling rate unchanged.

Some studies indicate that older mares are more prone to abortions for other reasons which could easily be aggravated by winter stress. Nishikawa and Hafez (1974) state that prenatal mortality is more frequent in lactating mares bred early in the season. This is applicable to the Red Desert situation, as most of the older females were lactating and also foaled early in 1978. In older mares embryonic loss may also be due, in part, to uterine atony (Hafez and Jainudeen, 1974). Nett (Department of Physiology and Biophysics, Colorado State University, Fort Collins; pers. comm.) says that hormone levels tend to be lower in older mares. Thus they would tend to be more susceptible to the hormonal deficiencies mentioned by Nishikawa and Hafez (1974) as a source of abortions. Nishikawa and Hafez (1974) state that abortion rates are lowest in mares three to six years of age.

Evidently several of the aged mares on the study area did fare poorly during the winter, as they were very gaunt at the start of the foaling season and none of them foaled. For one of these mares this was the first time in at least four years that she had no foal.

Another interesting age-specific effect was seen in the 1979 dates of foaling. A third of the older mares who foaled in May of 1978 did not foal until late in 1979. For instance, one older mare gave birth in mid-May of 1978. In 1979 she foaled in late August. Perhaps the gestation period of older mares might be longer than eleven months. However, Rossdale and Short (1967) report only a slight tendency for lengthened gestation in older domestic mares and the duration was only increased an average of two days. The poor condition of aged animals might also prolong gestation; however, Howell and Rollins (1951) found that nutritional status accounted for only 5% of the total variation in gestation length. Mares on subsistence rations had gestations which were only four days longer than those who were well-fed. More variation (44%) was explained by the season in which the mares were bred. Those that conceived between December and May carried their foals for 10.4 days longer than those bred from June to November. Similarly, Hucko (1961) found gestation to be eight days longer for mares bred in the spring as opposed to the autumn. He also found that male foals were carried .6 - 1.8 days longer than females. Even if all these factors were additive, old undernourished mares bred in the spring and carrying male foals would only lengthen their pregnancy a maximum of 18 days. This means that the mares would still have to be cycling several times to create the disparity in foaling dates for some older mares between the two years. About half the primiparous mares foaled in May of 1979. While the older mares are probably taking several estrous periods to conceive because of a build-up of stress from years of foaling and lactation, the younger mares cycle and are bred early due to their better physiological condition.

Nelson's (1978) data on feral horses of Carson National Forest, New Mexico, has relevance to the differences seen between the foaling dates of the older and younger mares in the Red Desert. In his study some mares had a higher nutritional status because of access to revegetated areas. These horses began foaling a month earlier and contributed more foals to the population than those without access to those early green-up sites. The early foaling dates and higher natality evident in those mares with access to revegetated areas seems to parallel what probably happened with the younger mares in 1979 on the Red Desert, which are probably in a better physiological state than their aged counterparts.

Birth Histograms

Tables 4 and 5 show births during the 1978 and 1979 foaling seasons, respectively. Known births are listed by herd and date. These tables were used to calculate minimum percentages of the season's foal crop present at the end of each month. It must be emphasized that these are minimum percentages, because foals of unknown birth date present in a herd sighted for the first time in July might actually have been born in March, April, May, or June. This is especially true for the 1978 season, as unusually late snows in the spring delayed much of our herd location work until June. In 1979 we searched consistently at an earlier date, and the calculated percentages of foals present at the end of each month are closer to the true distribution of births. The larger sample size in 1979 permitted the construction of a histogram of known births from April through August (Figure 2). The majority of the foals were born in May and June.

Sex Ratios

The 1978 sex ratio of foals for which a gender was ascertained was two males to one female. I believe this was due to the relative ease with which males are sexed and to my inattention to this subject in 1978, rather than to any aberration on the foals' part, especially since their ratio as yearlings was 1.16 males to one female. In 1979 I was more assiduous in determining the sexes of the foals and the ratio was 1.05 males to one female.

Foal Mortality

An estimate of age-specific mortality was obtained using foal carcasses found during the study (Table 6). If a foal less than three or four months of age disappeared from its mother's side it was also counted as a death. The 1979 portion of the table is almost meaningless since so few foal deaths are known. In 1978 it can be seen that a comparatively large loss of foals occurred in the first week of life. Foals may be born weak, but even healthy ones are vulnerable at this time while imprinting on their mother and still awkward of movement. Again, the number of deaths within the first week of life is probably conservative, since foals in this age bracket may have died before I even realized they were born.

There are fewer deaths as the foals grow older. The last age bracket from six months to one year is, of course, a longer time span than the other age groupings. Over half the dead foals in this age bracket were "winter kills" during the harsh 1978/1979 winter, and in a normal year this number would proably be much lower.

Table 6 also shows the sources of the previously mentioned deaths. Coyotes and golden eagles are the only potential predators on the study site, but were never known to bother foals. There were quite a few unknown causes of death, but two of these deaths were probably due, in large part, to inexperienced mares. Both of these mares had foaled for the first time and were inattentive to their foals. One of the desertions was probably also attributable to the inexperience of the mare.

Desertions are particularly interesting because in some instances they are indirectly an effect of weather on the population. Little rain falls during the summer in the desert and the ponds at the artesian wells begin to disappear. Water then becomes a limiting and much sought resource. When large concentrations of horses gather at these dwindling water sources, milling and confusion result. In two years there was one desertion caused when a foal became separated from its mother under such circumstances, and 17 instances where the foal was only temporarily lost. If the horse population is allowed to grow unchecked without an increase in access to water, incidents of separation and desertion will probably rise and may serve as a form of density-dependent population control. Of course, before desertion becomes a very important controlling factor, it would probably be eclipsed by deaths from dehydration.

Implications for Management

If the population of horses is allowed to continue to grow without an increase in access to water, their numbers may eventually be controlled by density-dependent deaths due to dehydration and foal desertion. This is probably not a desirable method of population control in that livestock and other wildlife would also be adversely affected.

The other alternative is to remove excess horses. Since natality and foal survivorship of feral horses in the Red Desert is high, this requires that substantial numbers of horses be removed in order to curb population growth. As natality and survivorship appear to be greatly affected by the severity of the winter, consideration of the previous year's weather patterns will be important in determining exactly how many horses should be removed.

Since most mares foal every year and may be bred by more than one male (Miller, 1980), removing or sterilizing females will have more of a curbing effect on population growth than manipulating the males.

The main foaling season extends from late March through August and foals are especially vulnerable in their first week of life. Therefore, roundups of excess horses should not take place during this period in order to avoid stress to near-term mares and very young foals.

Because foals are easily trapped in mud and improperly maintained fences, managers should be required to properly maintain areas around stock holding and watering facilities, and drilling sites.

Summary

1. In 1978 and 1979 the mare-foal demography of a population of feral horses in Wyoming's Red Desert was studied.
2. A small sample of long-term data indicates that most adult mares foal every year; however, this yearly foaling cycle was disrupted in 1979 by a severe winter.
3. Natality and foal survivorship were generally high; however, there was a significant difference between the 1978 and 1979 data. Abortions and stillbirths after the severe 1978/1979 winter are believed to have been responsible for the reduction of natality by one-third in 1979 as compared to 1978. Abortions and stillbirths probably also account for the seemingly higher foal survivorship of 1979, because the weaker fetuses would have died and their carcasses been scavenged before their births could be noted. Only healthy foals likely to survive would have been seen.
4. No mares younger than three years foaled. Three-year-olds have a lower foaling rate than adults.
5. Very old mares were more affected by the severe winter than younger mares, as they were gaunt at the start of the foaling season and did not foal.
6. Some older mares appear to be cycling several times before conceiving, since they foaled later in 1979 than in 1978. This is probably due to a buildup of stress from years of consecutive foaling and lactation. Primiparous mares conceive and foal earlier due to their better physiological condition.

7. The foaling season extends from late March through August with a peak in May and June. A few foals are born throughout the rest of the year.
8. The sex ratio of both foals and yearlings is approximately one to one.
9. The majority of foal deaths occur in the first week of life.
10. Sources of foal mortality include a weakness at birth, inexperienced dams, desertion or separation from the dam, bogging down in mud, being hit by cars or caught in fences, or dying of winter debilitation. The milling of large concentrations of horses at dwindling water sources in summer results in foal desertions. These may eventually become a density-dependent population control if they are not superseded by density-dependent deaths from dehydration.

Acknowledgements

Richard Miller deserves special thanks for his help and advice throughout all phases of this study. Dr. Lyman McDonald of the University of Wyoming provided much needed aid with the statistical analyses, and Dr. R. H. Denniston, my advisor, should be mentioned for his patience and support. I am grateful to Dr. Tom Dunn, Dr. Jim Waggoner, and Dr. Dave Yates of the University of Wyoming; and Dr. Ed Squires and Dr. Terry Nett of Colorado State University for taking the time to answer my questions concerning nutrition and reproduction in horses. Richard Miller, Dr. Mark Boyce, Dr. Lyman McDonald, and Dr. R. H. Denniston were all kind enough to review this manuscript.

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Table 1. Monthly Climatological Data for the Rock Springs Area

Month	Average °C		Departure from normal, °C		Total snowfall in inches		Max. accum. on ground, inches	
	77/78	78/79	77/78	78/79	77/78	78/79	77/78	78/79
Nov.	0.0	-4.1	+2.3	-11.0	9	22.1	6	10
Dec.	-2.4	-10.8	+9	-18.0	4	12*	4	8*
Jan.	-4.4	-14.0	+8.8	-22.3	16.2	16.3	8	14
Feb.	-2.5	-4.3	+7.4	+1.6	12.6	3	8	14
March	+3.1	+0.3	+15.7	+6.5	5	4.4	3	3

Data collected by the Federal Aviation Agency at the Rock Springs airport 40 km southwest of the study site and referenced in Climatological Data, Wyoming monthly summaries, Volume 86 numbers 11-12; Volume 87 numbers 1-3 & 11-12; and Volume 88 numbers 1-3. U. S. Dept. of Commerce, National Oceanic and Atmospheric Administration, National Climatic Center, Asheville, NC.

* No record of snowfall was made during this month from the Rock Springs airport. Values shown were noted for the town of Rock Springs about 7 km west of the airport.

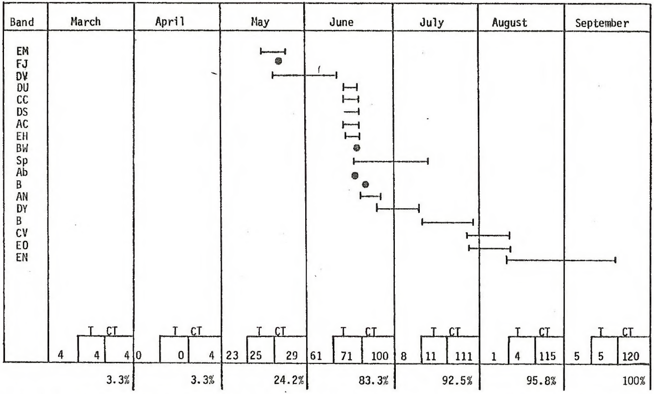
Table 2. Comparison of Natality and Foal Survivorship for 1978 and 1979

	1978	1979	Significance level on the difference	95% Confidence interval on the difference
Natality	n=373 horses	n=398 horses		
Foals per 100 other horses	29.5 (22.8%)	21.7 (17.8%)	p<.01	5.0 ± 4.0
% 3-year-olds and older foaling	78.1	52.6	p<.0005	25.5 ± 8.7
% 4-year-olds and older foaling	86.3	54.5	p<.0005	31.8 ± 8.4
Foal survivorship	n=51 foals	n=43 foals		
% survival to one month	86.3	100.0	p<.0005	12.7 ± 7.1
% survival to two months	82.4	97.7	p<.0005	15.3 ± 8.0
% survival to one year	82.4			

Table 3. Comparison of Foaling Rates With and Without Three-Year-Olds

	With 3-year-olds	Without 3-year-olds	Significance level on the difference	95% Confidence interval the difference
1978	78.1%	86.3%	p<.05	8.2 ± 7.1
1979	52.6%	54.5%	p<.05	1.9 ± 7.2

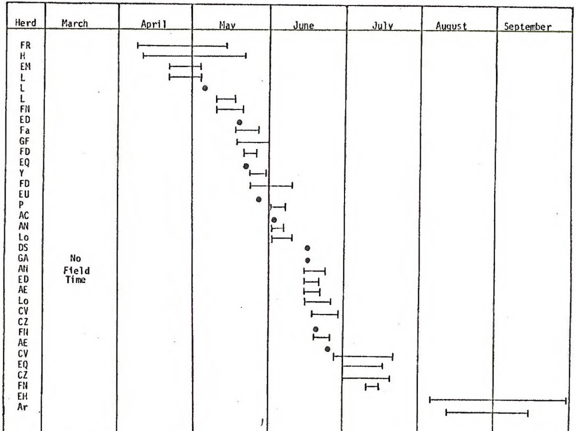
Table 4. Births - 1978 Foaling Season



	March	April	May	June	July	August	September
	4	0	23	61	8	1	5
T	4	0	25	71	11	4	5
CT	4	4	29	100	111	115	120
	3.3%	3.3%	24.2%	83.3%	92.5%	95.8%	100%

Bars indicate a range of days in which the foal was born; dots indicate precisely known dates of birth. The number in the lower left corner of each column gives the foals already present when their bands were located for the first time that year. Box T adds this number to the number of foals whose range of birth falls at least half into that month. Box CT is a cumulative total along the months and is used to calculate the minimum percent of the season's total foal crop present at the end of each month, as given along the bottom row of the table.

Table 5. Births - 1979 Foaling Season



	March			April			May			June			July			August			September		
		T	CT		T	CT		T	CT		T	CT		T	CT		T	CT		T	CT
	–	–	–	6	10	10	40	50	60	20	35	95	3	7	102	3	4	106	0	1	107
	–			9.4%			56.1%			88.8%			95.3%			99.1%			100%		

Bars indicate a range of days in which a foal was born; dots indicate precisely known dates of birth. The number in the lower left corner of each column gives the foals already present when their bands were first located that year. Box T adds this number to the number of foals whose range of birth falls at least half into that month. Box CT is a cumulative total along the months and is used to calculate the minimum percent of the season's total foal crop present at the end of each month as given along the bottom row of the table.

Table 6. Foal Mortality

	1978 n=19	1979 n=3
Known deaths by age		
birth to 1 week	5	1
1 week to 1 month	5	1
1 month to 3 months	3	1
3 months to 6 months	1	
6 months to 1 year	5	
Sources of mortality		
unknown	5 (1= inexperienced mare?)	2 (1= inexperienced mare?)
winter debilitation	4	
weakness at birth	3	1
mud	3 (+ 1 near miss)	(1 near miss)
desertion	2 (1= inexperienced mare?)	
caught in fence	1	
hit by a car	1	

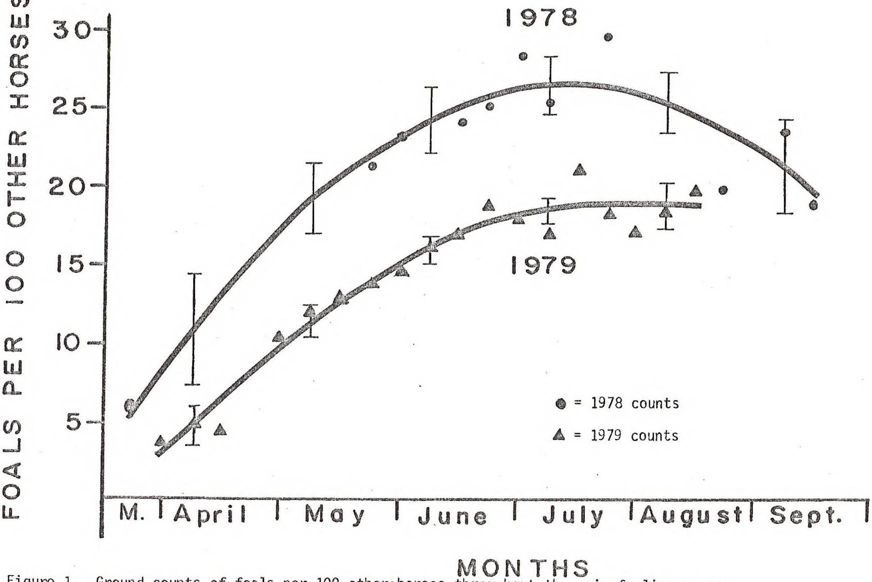


Figure 1. Ground counts of foals per 100 other horses throughout the main foaling season.

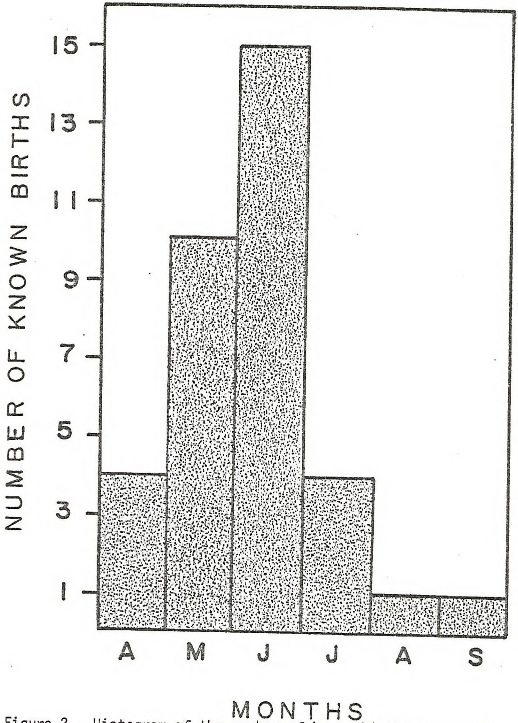


Figure 2. Histogram of the number of known births per month from April through September of 1979.

Population Ecology of the Kulan

Michael L. Wolfe
Department of Wildlife Science, Utah State University, Logan

Abstract

Close to extinction 50 years ago, a remnant population of kulan (Equus hemionus) has been protected in a Soviet nature preserve since 1941. From an initial population 200-300 animals, the population increased to approximately 2,000 in 1978. The implied average annual rate of increase (5-6 percent) is approximately two-three times lower than the purported rates among feral equid (E. caballus and E. asinus) populations in western North America. This paper summarizes demographic parameters of this kulan population based on a review of the Russian literature as well as the author's field observations.

Introduction

Population Ecology of the Kulan

The kulan is one of the five or six geographic races of the Asiatic wild asses, collectively known as onagers (Equus hemionus)[1]. The species' original (historic) range encompassed virtually all of the vast steppe and desert-steppe region of Central Asia. The northern boundary of this extensive distribution extended from the Ural Mountains through the steppes of Kazakhstan and Siberia east to Lake Baikal and the Gobi Desert. On the south onagers occurred in Anatolia (in Homeric times) through the deserts of Palestine, Arabia, Persia, Afghanistan, and Pakistan into the Thar Desert of northwestern India. Human exploitation and habitat destruction drastically reduced the numbers of these animals; presently they exist only in remnant populations on a fraction of their former range (Fig. 1). The largest of these segments is in Mongolia. Bannikov (1975) estimated the total number of onagers in the Mongolian Peoples Republic at about 15,000 animals, of which roughly one-half live in the Trans-Altai Gobi Desert. Another smaller population (perhaps 3,000) occurs in the deserts of Dasht-i-Lut and Dashti-i-Kevir in Iran. The Little Rann of Kutch, a salt desert area of some 2,600 km^2 on the frontier between India and Pakistan harbors another small population of onagers. This population undoubtedly suffered as the result of hostilities between the two countries. In 1962 there had been an estimated 870 animals in the Little Rann (Gee,1963); an aerial count made at the end of 1969 revealed only 368 (Groves, 1974). Bannikov (1975) reported a figure of 250 animals as the 1974 population level.

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[1] The taxonomic status of the Asiatic wild asses remains the subject of considerable controversy. Most authorities recognize a single species (Equus hemionus) that comprises five (Ellerman and Morrison-Scott, 1951; Haltenorth and Trense, 1956), six (Harper, 1945, Heptner et al., 1961); or even seven (Dennler de la Tour, 1975a, 1975b) living geographic subspecies. These include all the forms that are designated by their local vernacular names: ghor-khar, kulan, dziggetai, and kiang. Groves (1974), however, ranks the Tibetan wild ass or kiang as a species (E. kiang) separate from the lowland forms (onagers), based on differences in appearance, behavior, and climatic tolerance.

Perhaps the best known of these remaining populations lives in the Badchys Nature Preserve, located near the Iranian and Afghan borders in southeastern Turkmenia (Fig. 2). The preserve was established in 1941 for the protection and rehabilitation of the only remaining kulan (E. h. kulan) population in the Soviet Union. This population has increased from an estimated 200-300 animals at the time of the preserve's establishment to some 2,000 in 1978 (Kuznetsov, personal communication). Probable inaccuracies in these figures notwithstanding, the implied rate of increase in this population lies between 5 and 6 percent per annum. This growth rate is two-three times lower than the purported rate of increase among populations of feral equids (E. caballus and E. asinus) in western North America (cf. Cook,1975).

In 1953 eight kulan from the Badchys were introduced to Barsa-Kelmes, an island Nature Preserve in the Aral Sea in northern Kazakhstan. By the mid-1960's that population had increased to approximately 45 animals (Solomatin, 1973) and in 1977 the same author estimated the population at approximately 100.

The habitats occupied by kulan in these locations are analogous in terms of physiognomy, climate and vegetative life-form to some of the desert environs of feral equids in the southwestern United States. Given these similarities, an examination of kulan ecology should be informative from a comparative standpoint and may provide some insight with respect to the potential for natural regulation of North American feral equid populations.

The Badchys kulan population has been the object of extensive ecological and behavioral research by numerous Soviet scientists, notably V. I. Kravchenko and E. I. Shcherbina, V. G. Heptner, A. G. Bannikov, and A. A. Sludski. However, A. O. Solomatin's (1973) monograph, entitled "Kulan", represents the single most comprehensive treatment of onager biology. In this work Solomatin reviewed the findings of earlier investigators and presented the results of his own research, most of which was conducted while he was director of the Badchys Preserve. Unfortunately, most of these studies were descriptive--or at best semi-quantitative--in nature,and the data were collected during the 1950's and early 1960's. Klingel (1977) described briefly the social organization and behavior of kulan, based on limited observations made in the Badchys in 1973. Finally, Rashek (1959, 1972, 1973, 1975) has described various aspects of the ecology of the Barsa-Kelmes kulan population.

In the following paper I will attempt to summarize the current state of knowledge on the ecology of the kulan (particularly with respect to its population biology), based on a review of the Russian literature as well as my own limited field observations, made during the course of a two-week visit to Turkmenia in May, 1978.

My trip to the Soviet Union was sponsored by the National Academy of Sciences under the auspices of its Inter-Academy Exchange Program. I am indebted to the staff of the Badchys Preserve, in particular its

Director, V. I. Kuznetsov, and to Professor A. O. Tashliev, Dr. C. Ataev, and O. Atadzhan of the Institute of Zoology, Turkmenia Academy of Sciences, for their logistical support, accompaniment, and gracious hospitality during my visit to Turkmenia.

The Badchys Ecosystem

Ecologically, the Badchys bears numerous similarities to certain areas of the North American Intermountain West. The preserve encompasses an area of approximately 880 km^2 between the Murgrab and Tedzhen Rivers at the extreme southern edge of the Kara-Kum Desert. It is situated approximately 125 km west of Kushka, the southernmost city in the Soviet Union. Geomorphically, the Badchys is classified as a distinct province of the "Pre-Asiatic Upland" region (Bogdonova and Murzaev, 1968). An extensive upland tract with an average elevation of 800 m, the preserve's predominantly hilly (fossil dunes) terrain is interrupted on the west and north by relatively low-lying desert mountain ranges. Two large basins, Er-Oylan-Duz and Namak-Saar, constitute prominent features of the Badchys topography on the eastern and southern periphery of the preserve. The former and larger of these two depressions is approximately 10 km in width with an average depth of 400-500 m and extends some 20 km from east to west. It contains a very shallow salt lake, broken by several large, rocky outcrops. A river, the Egri-Gek, with perhaps the highest salinity of any river in the Soviet Union is also located in the preserve.

Hot summers, low precipitation rates, winters that are comparatively severe for its southerly lattitude (35-36°), and strong winds characterize the climate of the Badchys (Bannikov, 1961). Temperature extremes range from -30°C in winter to 48°C in summer. Like desert environments in other locations, the amplitude of diurnal temperature fluctuations may be as great as 21-22°C. Annual precipitation averages 25 cm but varies significantly (10-46 cm) from year to year. The bulk of the precipitation falls in the month of March, with virtually none occurring from May to October. Winter snow depths seldom exceed 50 cm and normally lie within the range of 10-30 cm. Because maximum daily temperatures (even in January) usually exceed the freezing point, snow cover rarely persists for more than three-ten days at a time. The winds in the Badchys blow with amazing constancy, but frequently shift directions in the course of the day and throughout the year. They usually reach peak velocity during the mid-day hours. The name "Badchys" is literally translated as "where the wind rises".

The vegetation of the Badchys is best characterized as a shrub-steppe. The desert climate and prevailing aeolian soils of the preserve support a vegetation consisting primarily of low-growing perennial and annual grasses (mainly *Poa bulbosa* and *Bromus* spp., respectively), sedges (*Carex* spp.), numerous ephemerals and some perennial forbs, including several species of *Astragulus*. Some of the more conspicuous perennial plants belong to a monocarpic umbelliferous genus (*Ferula* spp.) that live for four-five years. Five species of *Ferula* occur within the preserve, one of which may obtain a height of 2.0 m. With the exception of pistachio (*Pistacia vera*), which grows in higher locations of the preserve, the landscape is largely treeless. Consequently, pistachio trees play a prominent role in the local ecology for the shade they provide from summer heat, as a food source (nuts), and as nesting sites for some raptors and carrion-feeding birds. In past years the Badchys enjoyed a peculiar dual status, being a nature preserve and at the same time a "kolkhoz" (collective farm). Thus, pistachio nuts were harvested commercially and some plantations were established within the preserve. Some of the more common shrubs and half-shrubs include Lygophyllum spp., Artemisia spp., Salsola spp., and Atriplex spp. Black saxaul (Haloxylon aphyllum), and tamarisk (Tamarix sp.) occur locally in riparian and other mesic habitats.

Given its desert character, the mammalian fauna of the Badchys is surprisingly diverse, comprising some 40 species. In addition to the kulan, the preserve is inhabited by at least 3,000 mufflon or argali sheep (Ovis ammon), perhaps as many as 4,000 djeran or goitered gazelles (Gazella subgutturosa), and unknown but probably lesser numbers of wild goats (Capra aegagrus), and even wild boar (Sus scrofa). The larger predators that still occur in the preserve include the wolf (Canis lupus) and leopard (Panthera pardis).

Kulan Population Dynamics

As noted previously, reliable demographic data on the kulan are virtually lacking. A crude approximation of the growth rate of the Badchys population is shown in Fig. 3. The growth curve was derived from regression analysis (exponential model) of the estimated number of animals present in the preserve in the years 1941, the late 1950's (based on data from Solomatin, 1973), and in 1973 (Klingel, 1977) and 1978 (Kuznetsov, personal communication). It should be noted that during the period 1946-1959 a total of 70 foals were removed from the population for reintroduction to other locations. Undoubtedly, these removals had some effect on the growth rate of the population. However, the actual number of animals removed (1 - 10, $\bar{x} = 5$) in any given year was small in comparison to the total population, and the effect is probably masked by the questionable validity of the individual population estimates. The data do indicate a comparatively slow annual rate of increase (approximately 5 percent per annum).

In terms of reproductive biology, onagers do not differ appreciably from other members of the genus Equus (cf. Klingel, 1969). Most mares produce their first foal in their fourth year of life (Solomatin, 1973; Treus and Lobanov, 1974; Rashek, 1975). Based on 1423 observations made in the Badchys in April and May (i.e. during parturition) in 1959, Solomatin reported that potentially partus females comprised 24.2 percent of the total animals classified. Of these females 75.5 percent were either pregnant or accompanied by recently born foals. The product of these two percentages would indicate a potential foal crop of approximately 18 percent. Such a computation is confounded by the fact that Solomatin's classification incorporated a substantial number of duplicate observations. This is obvious from the fact that the total sample size was approximately twice the total estimated size of the Badchys population in 1959. Furthermore, the foaling season was already in progress and Solomatin's (1973) published data are insufficient to separate out the number of foals in the total sample.

Turkmenian kulan exhibit a greater synchrony of foaling than that of feral equids in North America. In the Badchys most births occur between 15 April and 14 May, the peak falling about 25 April. The earliest and latest occurrences of newborn foals were observed on 8 April (1951) and 28 July (1947), respectively. On Barsa-Kelmes the parturition period extends from mid-May to the end of June (Valentina, 1964; Rashek, 1975). These foaling periods are generally earlier and of shorter duration than those reported by Harper (1945) and Gee (1963) for Baluchstan and the Little Rann of Kutch, respectively. In these more southerly regions the foaling period extends from June and July through August and even into September. These limited data suggest the possibility of an inverse correlation between increasing latitude and the approximate duration of the parturition period.

Table 1 summarizes the foal crops in the Badchys population as estimated from composition counts conducted during the months of August through October in several years. The unweighted and weighted mean foal complements were 15.2 and 16.7 percent, respectively. These figures are quite comparable to extrapolated late-summer foal complements among feral horse populations in North America (vide: Wolfe in press).

Solomatin's (1973) figures suggest that a substantial first-year mortality rate may represent the major determinant of the apparent slow rate of population growth for the Badchys kulan population. Based on his population projections, the mean complement of foals in the population shrinks from an estimated 19 percent immediately following parturition to approximately 14 percent by fall. By April of the following year, foals comprise a mere 9 percent of the pre-parturition population. These figures indicate post-natal and overwinter survival rates of 74 and 64 percent, respectively. Accordingly, the total first-year survival rate is barely 50 percent. Solomatin suggests lack of water and substantial winter losses as the primary factors responsible for this mortality.

As noted above, eight kulan from the Badchys were introduced onto Barsa-Kelmes Island in 1953. Between 1953 and 1964 this initial transplant was augmented by an additional 11 animals. The growth of this population, in contrast to that of the Badchys, is distinctly sigmoid in nature. Excluding subsequent introductions the initial population increased to 47 animals by 1963 and thereafter appeared to stabilize at about 43 animals. During the period 1956 to 1967 a total of 78 foals were produced, with a mean annual foal crop of 19.7 percent of the post-parturition population. However, the total mortality sustained by the entire population during the same period was 57 animals or approximately 73 percent of the cumulative increment. It is noteworthy that 95 percent of the total mortality occurred after the population peaked in 1963. Many of the animals examined showed extensive hemorrhaging of the intestinal wall.

This evidence suggests that the Barsa-Kelmes population may have reached its carrying capacity in the early 1960's, this occurring on an island devoid of large predators. There remains the problem of Solomatin's (1977) estimate of 100 animals for Barsa-Kelmes; he failed to cite the source or reliability of this later estimate. Even conceding that approximately 100 kulan did in fact inhabit the island in 1977, the implied average annual rate of increase from the 39 animals present in 1967 would only represent 10 percent.

Mortality and Potential Limiting Factors

Several larger predators inhabited the original range of the Asiatic wild asses, notably the wolf, leopard, and even the tiger (Panthera tigris). Of these only the wolf can be considered as a potentially significant predator. However, in comparison to the losses inflicted by wolves on other ungulates, the impact of wolf predation on kulan is relatively minor. In a band the animals are relatively invulnerable by virtue of their speed. Even a single mare will defend its foal actively and frequently successfully against attack by wolves. Nonetheless, Heptner et al. (1961) maintain that a fair number of foals do fall prey to wolves--especially when in a weakened condition during severe winters. Occasional predation of young foals by golden eagles (Aquila chryseatos) has been reported by Solomatin (1977). Weighing the admittedly limited evidence available, it is my conclusion that predation by itself does not constitute a limiting factor for kulan, except possibly when population levels are very much depressed.

Winter losses may constitute a significant source of kulan mortality. Quantitative data on the magnitude of such losses are lacking, but Sludski (1953, 1963) cited exceptionally severe winters of 1879/80 and 1891/92 as a major cause for the disappearance of the kulan in Kazakhstan. According to Solomatin (1973) the kulan can withstand extreme winter temperatures and it can forage and move in relative freedom in loose snow, the depth of which does not exceed 30 cm. However, protracted periods of deep snow (>40 cm) or snow of high density or with crusted surface conditions will result in substantial winter losses. Under these conditions the chill factor associated with extremely low temperatures and high wind velocities aggravate the problems of obtaining forage and thermoregulation and cause even greater losses. Such conditions occur relatively infrequently in southern Turkmenia in comparison to other portions of the onager's former range. Within the span of approximately the past half century, the most severe winter occurred in 1934/35, and occasioned drastic losses in the Badchys kulan population (Ischunin and Korovin, 1945).

As is the case with other equids, the availability of water appears to represent an important limiting factor for the kulan. In this respect the Badchys does not comprise a complete ecological unit for its kulan population. Virtually all of the natural water sources in the preserve dry up in the summer and the salinity of the four that remain generally precludes extensive use by the kulan. Solomatin's observations indicate that kulan will not utilize water with a salt content of greater than 20 g per liter. Lactating females will reject water with a salinity of 10 g or more per liter. Consequently, a substantial fraction (60-80 percent) of the population migrates out of the preserve annually (as far as 100 km) to spend the dry season along the Kushka, Tedzhen, and Murgab Rivers. These observations are not consistent with those of Rashek (1975), who noted that although kulan on Barsa-Kelmes prefer fresh water, they will also drink the brackish (salinity = 10.8 percent) water of the Aral Sea.

Most authors list a variety of herbivores as potential competitors with onagers for both forage and water. These include the native ungulates listed above that share the Badchys ecosystem with the kulan.

However, for the most part, competition for forage between the kulan and these indigenous ungulates is not considered significant. In other portions of the species' original range and under pristine conditions both the saiga antelope (Saiga tatarica) and the Mongolian gazelle (Procapra gutturosa) may have competed with onagers for forage to an unknown degree.

More serious competition for forage occurs between the kulan and smaller herbivores. The severity of this competition varies considerably from year to year as a function of several factors, the most important of which are annual precipitation rates and forage production as well as the densities of the competing herbivores. Mambetzhumaev (1969) noted competition between susliks (Citellus fulvus) and kulan as well as saiga antelope--particularly under drought conditions--on Barsa Kelmes. Solomatin (1973) considered gerbils (Rhombombys sp. and Meriones sp.) and a tortoise (Testudo horsfieldi) as the most significant competitors for food with the kulan in the Badchys. That populations of these competing herbivores may reach very high densities is illustrated by the following scenario, described by Solomatin for the drought year 1960. In that year total forage production was estimated at approximately 200 kg/ha. At the same time, the density of tortoises approached 80 per ha in some locations, with an estimated daily forage removal of 100 g per animal per day. Gerbils show recurring population fluctuations, and when a population peak coincides with a drought year, serious competition may result. For example, Solomatin (1973) reported a mean of 45 greater gerbil (Rhombombys opimus) colonies per ha for the year 1962.

Domestic livestock, especially sheep, are generally regarded as the most serious competitors with kulan for both food and water. Presently, livestock grazing is not permitted within the Badchys Preserve, but Solomatin (1973) reported that as many as 20,000 sheep are grazed annually in an area of 90 km^2 along the Kushka River that is utilized by approximately 500 kulan in the summer months. Bannikov (1975) implicated domestic livestock as the major determinant responsible for the continuing decline of onagers in Mongolia and other portions of their former range.

Other factors, notably poaching losses, may constitute a significant source of kulan mortality. Solomatin (1973) cited poaching as the cause of death for 33 percent of 118 kulan remains found in the Badchys between 1934 and 1962. This figure probably does not adequately reflect the actual magnitude of poaching losses.

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Table 1. Foal complements in the Badchys kulan population, estimated from late summer classification counts.*

Year	Sample size	% Foal Crop
1952	156	12.2
1954	159	15.1
1955	157	13.4
1956	363	15.4
1957	592	19.9
Unweighted mean		15.2
Weighted mean		16.7

*Based on data from Solomatin (1973)

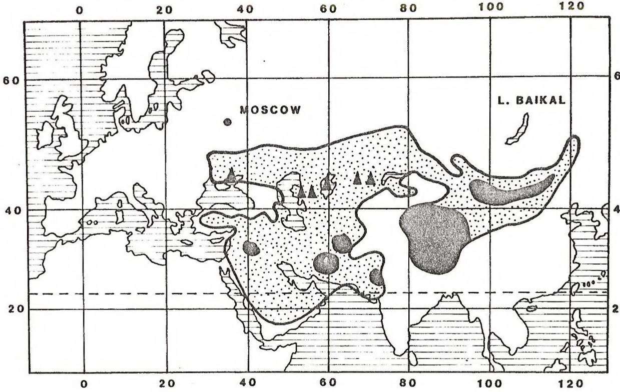
0
20
40
60
80
100
120
60
40
20
MOSCOW
L. BAIKAL

Figure 1. Past and present distribution of Equus hemionus. Stippled area shows the extent of the species' original range. Shaded areas indicate the locations and approximate range of existing populations. Proposed sites of re-establishment are designated by black triangles.

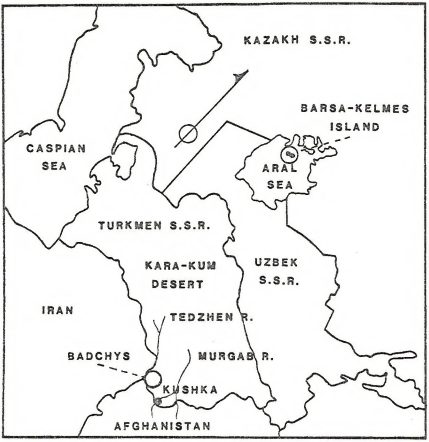
KAZAKH S.S.R.
BARSA-KELMES ISLAND
CASPIAN SEA
ARAL SEA
TURKMEN S.S.R.
KARA-KUM DESERT
UZBEK S.S.R.
IRAN
TEDZHEN R.
BADCHYS
MURGAB R.
KUSHKA
AFGHANISTAN

Figure 2. Map of Central Asia, showing locations of the Badchys and Barsa-Kelmes Nature Preserve and other pertinent geographic features.

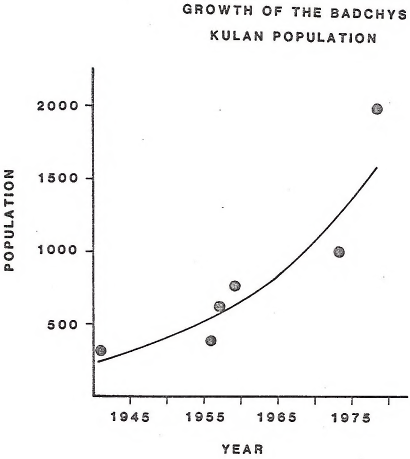

Figure 3. Growth of the Badchys kulan population.

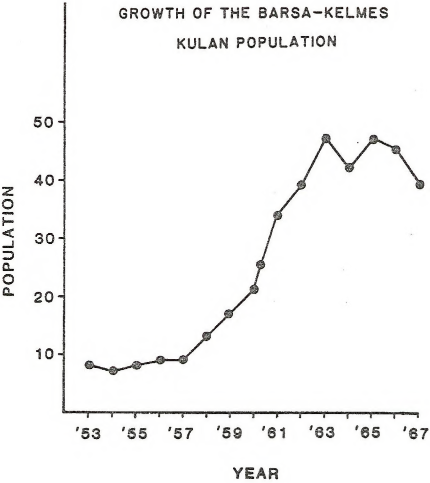

Figure 4. Growth of the Barsa-Kelmes kulan population.

Population Dynamics of a Herd of Feral Burros

Susan L. Woodward
Department of Zoology, Arizona State University, Tempe

Abstract

In 1974 the feral burro population in the Chemehuevi Mountains of California had a recruitment rate of 28 percent, the result of 75 percent natality. Females had their first foals when age two, and then produced foals at an average rate of once every 16.2 months. It appeared that an irruption was following the complete protection accorded feral burros in 1971. However, when census data from 1958, 1971, and 1974 are analyzed, it is seen that the population has been growing at an average annual rate of 5 percent since 1958. The discrepancy between recruitment rate and annual rate of increase calls for examination of mortality rates and emigration as well as natality rates over a number of years. As yet there are few data on these parameters of burro population dynamics, but field observations indicate fluctuating natality rates and significant mortality among young males and adult females may be major factors.

The Potential for Increase in Horse and Ass Populations: A Theoretical Analysis

Walt Conley
Department of Fishery and Wildlife Sciences, New Mexico State University, Las Cruces

Introduction

The potential for increase has been a primary subject of interest to population biologists since the original essay by Malthus (1798). Even though population parameters that reflect rate of increase are intuitively appealing, and necessary for various applications of research, adequate estimates are difficult to obtain. There are various reasons for such difficulties, some of which are less admissable than others, which have led to a diverse literature that attempts to provide solutions for both analytical and estimation problems. In this paper, I deal primarily with the analytical and conceptual difficulties associated with rates of increase in animal populations. Much of the discussion to follow is general in that it applies to any biological population. However, I have chosen examples that reflect the sort of life history patterns seen in horse and ass populations. My purpose in so doing is to establish a series of theoretical boundaries for rates of increase in such populations; boundaries they are not expected to exceed. At the same time, I have provided a series of graphs that represent various combinations of the primary population parameters of survival and reproduction, in an effort to clarify the interactions that result in various observed rates of increase.

A theoretical approach of this form is important in that it establishes certain biological and mathematical "rules of the game." Additionally, given agreement on basics, a foundation is thus provided for the interpretation, and judgment of the worth, of available information pertaining to real populations.

The available literature on mathematical demography ranges from highly sophisticated and abstract to superficial and perhaps trivial. Within this body of literature, there exist presentations that are intermediate in mathematical complexity, and that are intended to facilitate understanding of the biological processes involved (e.g., Caughley, 1966, 1967a, 1967b, 1977; Cole,1954; Conley,1978; Eberhardt,1969; Mertz, 1970). Throughout, however, there are major problems involved with the appropriate estimation of demographic parameters from wild populations (see Pospahala et al.,1974; Anderson,1975).

Although problems of estimation are real, and associated implicit assumptions are highly restrictive, these two facts do not excuse the continued misuse of demographic techniques, nor do they excuse statements regarding "realized" rates of increase that are impossible even in a theoretical context, much less in the real populations being presumably described.

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It is not my purpose here to contribute to a discussion of the various interpretations available concerning "rates-of-increase" in populations. As a result, I have avoided such terms as "intrinsic rate of increase", "r-max", "malthusian rate of increase", etc.; for an entrance to this discussion see Caughley (1977), Conley (1978), Conley and Nichols (1978), and Slade and Balph (1974).

Methods

Specification of the Model

I have chosen to present rates of increase in the form of finite rates over specified, discrete units of time. Example life history patterns shown here typify those found in equid populations, i.e., patterns that apply to species that are iteroparous, long lived, single young per birth, extensive maternal care, and polygynous. Definitions and model structure follow Conley (1978).

A cohort is a group of individuals of the same age in a population. Given a cohort of age zero individuals (i.e., a group of new born), they can then be followed through time, and the pattern of survival can be determined. When the cohort is exhausted, the resultant pattern is converted into a schedule of survival probabilities by:

$$\ell_x = n_x/n_o, \qquad (1)$$

where x represents age, ℓ_x is the probability that an age zero individual will survive to enter the xth age class, and n_x is the number of individuals in the x to x+1 age class. Survival schedules are often sex-specific; for our purposes, I will deal only with the female portion of the population under the assumption that:

1) there are sufficient males to provide for the breeding demands of the females; and
2) that the sex-ratio at birth (expressed as proportion males) is one, and that survival probabilities are the same for males and females.

A fertility schedule for a population (m_x) typically reflects the expected production of daughter offspring for a female aged x to x+1. Conley (1978) has restricted this to those females that are actively producing young, and further defined the remainder as non-breeders. In this manner, the importance of whether or not a female breeds during any given time step becomes apparent.

Thus, putting β_x as the proportion of the females in the x to x+1 age class that do breed during the t to t+1 time interval, with ℓ_x and m_x as defined above, the finite rate of increase for a population at stable age distribution is given by:

$$1 = \sum_{x=1}^{\omega} \lambda^{-x}\ell_x m_x \beta_x \qquad (2)$$

with ω being the least age class that contains individuals, and λ the finite rate of increase.

The rate of increase, λ, may be obtained by the iterative solution of the polynomial in λ (equation 2), or by utilizing a compatible projection model and iterating time steps through attainment of stable age distribution.

In the latter form, the number of young entering the population at time t is given by:

$$n_{o,t} = \sum_{x=1}^{\omega} n_{x,t}\, m_x \beta_x, \qquad (3)$$

and the number of individuals entering subsequent age classes at the next time step is:

$$n_{x+1,t+1} = n_{x,t}\, p_x, \qquad (4)$$

where p_x is age-specific survival given by:

$$p_x = \frac{1 - \ell_x - \ell_{x+1}}{\ell_x}\ . \qquad (5)$$

It should be noted that rates of increase as expressed above are compatible with classical population theory (Lotka,1956; Hutchinson, 1978; Mertz,1970), but are not similar to current applications of matrix projections that stem from the works of Leslie (1945, 1948), Lewis (1942), and Bernardelli (1941), where recent usage has eliminated the originally defined F_x function (Leslie, 1945, 1948) and replaced it with a standard m_x schedule. It is beyond the scope of this paper to discuss these distinctions (see Goodman,1967; Keyfitz,1968).

Population Projections

The above model is programmed in FØRTRAN IV along with various extensions not essential to this discussion. Additional examples of the use of this model are given by Conley (1978), Conley et al. (1977); Lenarz and Conley (MS); Watts and Conley (MS); Nelson (1978); and Tipton (1975).

No attempt has been made for this presentation to extensively document life history patterns in feral equid populations. Much of the information required for an adequate analysis is simply lacking. There are, however, some aspects of feral equid biology upon which general agreement can be obtained.

Gestation period in the horse (Equus caballus) is about 330 days, with considerable variation being induced by seasonal or nutritional factors (Asdell,1964). In the ass (Equus asinus) gestation is 365 days (Asdell,1964). Twinning is particularly rare in E. caballus but does occur (Speelman et al.,1944; Feist and McCullough,1975), and is also of no demographic consequence in E. asinus. Breeding behavior typically begins not sooner than two years in E. caballus and one year in E. asinus, with subsequent birth occurring in the three- and two-year-olds, respectively. Information on breeding proportions is scanty; Nelson (1978) reported 55% of breeding age females (E. caballus) having foals; E. asinus appears to be comparable (Moehlman, pers. comm.). Assuming one young per year and a sex ratio of one, the basic m_x value was set at 0.5 for ages 2-14. Modifications to this schedule generally involved manipulations of the proportion breeding vector except for questions involving effects of age at first breeding.

Survival schedules are also difficult to find in the formal literature. Nelson (1978) constructed a tentative ℓ_x schedule for E. caballus from New Mexico, and Wolfe (MS) has attempted reconstruction of a series of age-structure patterns from various E. caballus populations. In general, both species appear to survive quite well, i.e., the ℓ_x curves are fairly flat prior to old age), and there is some suggestion that males "survive" less well than females (Nelson, 1978). This latter case may well be the result of differential migration in the males which superficially shows as mortality.

In order to keep the number of possible combinations of life history patterns within reason, I have chosen 14 years as maximum age; the effects of such a choice are discussed below.

Given the above general considerations, an extensive series of simulations were conducted that represent the various combinations of life history patterns of interest. Eight hypothetical survival schedules were constructed and each was matched against sequences representing various age-at-first-breeding, proportion breeding, reproductive life-spans, and maximum age patterns. All simulations were continued to attainment of stable age distribution, and subsequent finite rates of increase were thus obtained.

All simulations were conducted on the New Mexico State University Amdahl 470-V5 computer.

Results

The eight hypothetical survival schedules are shown in Fig. 1. Schedule 1 represents a theoretical maximum, with no deaths prior to maximum age 14. Schedules 2 through 8 simply represent successive decreases in survival rates.

Initially, an important decision involved what age to use for maximum age. Most large-animal populations are aged according to various tooth eruption and wear patterns. Such techniques typically provide somewhat less than satisfactory results through the stage where all teeth are at occusal level, and increasingly notorious results in older age animals. Thus, the question arises: "How important is maximum attained age in determining rate of increase?" The answer can be seen in Fig. 2, which suggests that knowing maximum age is not particularly important. The curves representing λ at various maximum ages inflect and tend to flatten at about age 14. This flattening effect would be even more pronounced given realistic survival schedules, where the proportion of older individuals in the population would be considerably less than that resulting from survival Schedule 1. It is this effect that led to the decision to use 14 as a "generalized-old-age"; the results described here would not be greatly different if this age were increased by several time units. The conclusion is that summarization techniques that combine older age classes for subsequent analysis are probably appropriate, and that accurate aging techniques for these categories would (even if available) simply provide a level of detail to which the rate-of-increase question is insensitive.

In contrast, it is often not appreciated how important age at first breeding (i.e., parturition) is in determining rate of increase. The four curves shown in Fig. 2 reflect rates of increase attained across various maximum ages, with breeding beginning in years two through five. Finite rates of increase at age 14 vary from approximately 1.2 to 1.35 and represent an increase in doubling time in the population by about a factor of two. The relative positions of the curves shown in Fig. 2 would remain for simulations conducted across the various survival schedules, but would of course be progressively lower overall. In a real population, one would expect differing proportions of the females to begin breeding at different ages, with the average age somewhere between three and five years depending upon species and conditions.

The question of whether post-reproductive individuals are important to rates of increase has been alluded to occasionally (Allee et al.,1949; Cole,1954; Wilson,1975; Tipton,1975), but little substantive data seem to exist.

In a similar vein as with the maximal age question, I have conducted a series of simulations that provide rates of increase for the eight survival schedules across varying reproductive spans (Fig. 3). Again, the curves tend to become flat at about age 10 or 11, suggesting that reproductive life span is important only when it is very brief, and progressively less important as it extends beyond six or eight years (i.e., ages 9-11). Thus, while it is important to have information on breeding ages, such information has a decreasing effect on rate of increase at older ages.

Distinguishing between the expected number of female offspring to be produced by a female who is producing, and those females who are of breeding age, allows considerable insight into the dynamics of population growth. The number of young a female of a given species can produce is a product of long-term evolution and involved considerations such as size of female and embryos, skeletal structure, physiological and energetic demands of the young and capabilities of the mother, extent of maternal care, and so forth. It is thus no mistake, from an evolutionary viewpoint, that both E. caballus and E. asinus typically have one foal per birth event. This being so, and assuming a sex ratio at birth of one, m_x values are 0.5 for all age classes where breeding occurs.

In contrast to the ultimate reasons why a species has a given expectation of young at birth, the determination of whether or not a female joins the breeding component is much more proximate, and involves ecological and behavioral information. Separating these factors in the above model through the use of the β_x vector thus focuses attention on the proximate causes involved in population potentials, even though, algebraically, the results are similar to those treated in a more standard fashion.

The effects of varying proportion breeding on rates of increase for seven survival schedules are shown in Fig. 4. These curves are quite steep, and provide evidence for the importance of determining proportion breeding in populations of E. caballus and E. asinus.

Given the various interactions of demographic variables shown in Figs. 2 through 4, and the resultant rates of increase, the question of interpretation becomes important. One device follows from the following argument. A standard procedure for representing the rate of increase in a population with respect to time is to put N_t as population size a time t, and r as the instantaneous rate of population increase. From this, it follows that:

$$dN/dt = rN,$$

which, integrating, is,

$$N_t = N_o e^{rt} \qquad (6)$$

Posing the question, "How long does it take for a population with a given r to double in size?" requires only that Equation 6 be expressed as,

$$2N_o = N_o e^{rt}, \qquad (7)$$

and solving for t, Equation 7 becomes

$$t = \frac{\ell n 2}{r}. \tag{8}$$

The relationship between r and λ (Conley,1978) is

$$\lambda = e^{r},$$

and

$$\ell n \lambda = r. \tag{9}$$

Combining the relationship shown in Equations 8 and 9, and solving Equation 8 for the range of λ values that represent those shown in Figs. 2 through 4, yields a graph of population doubling times as a function of λ (Fig. 5). As can be seen in Fig. 5, doubling times are quite short for $\lambda \geq 1.07$ (i.e., less than ten years). The ecological importance of these potentials is discussed below.

Discussion

The sensitivity of rates of increase to changes in various population attributes and life history patterns is a subject of considerable importance to attempts to estimate such rates from wild populations. Because the rate of increase is such a highly integrative parameter, incorporating information from all levels of the biology of a species, the final values obtained are often questionable; further, assumptions required by the mathematical structure are particularly restrictive, and often, appropriate data are simply impossible to obtain.

It is not my purpose to discuss techniques involved in the collection of adequate data; rather, I have attempted to evaluate a range of values for certain population attributes, and to define their relative contribution to the resultant finite rate of increase. At the same time, it is possible to establish theoretical limits as well as an intuitive guide to reasonable values in wild populations.

As can be seen from Figs. 1 through 4, the rate of increase is particularly sensitive to: 1) the shape of the survival function; 2) proportion of the adult female population that actually produces young; and 3) the age at first breeding. In contrast, the rate of increase is relatively insensitive to: 1) maximum age attained by the breeding females; and 2) the presence of post-reproductive animals. The latter two attributes have a decreasing effect, and within our abilities to estimate ages and breeding span in wild popualtions, can be effectively ignored past beyond about 14 years of age and six to eight years reproductive life, respectively.

The survival patterns shown in Fig. 1 represent an array of possible patterns, but are probably too simple to be related directly to wild populations. It is reasonable to expect higher age-specific mortality in the zero age class (i.e., probability of surviving from x=0 to x=1). While such patterns could be simulated, the number of combinations would increase drastically. Thus, the patterns evaluated in this study, with their resultant rates of increase, must be considered as generally conservative. This is particularly true of Fig. 2, where only the theoretical maximum survival schedule was utilized.

The question, "What values for finite rate of increase can be reasonably expected in wild populations?" can be partially answered. Assuming that female survival schedules in wild populations are approximately similar to Schedule 4 in Fig. 1, and that proportion breeding is in the order of 50% or 60%, finite rates of increase of about 1.05 are to be expected.

Additionally, if survival schedules in the males are lower than those of females, then the results presented here are higher than would be obtained in wild populations. Again, the λ values presented here are conservative.

Finite rates of increase higher than 1.20 can only be obtained (see Figs. 3, 4) if the real survival schedules are similar to Schedules 1, 2 or, 3 (Fig. 1) and if the proportion breeding is 0.8 or greater across all age classes, and if age at first breeding is three years, and if breeding span beginning at age three, extends beyond about age eight to ten. Although adequate data do not currently exist to provide a definitive answer, the conclusion from data that are available is inescapable; empirical values for the various population attributes considered here are simply too low to conclude that rates of increase in wild populations approach 20%, much less exceed that level.

The presentation of population doubling times across various finite rates of increases (Fig. 5) is designed to illustrate the point that even at rates of increase between 1.01 and 1.10 (i.e., 1% to 10%) populations with similar demographic patterns do increase, with the relative concern that must be attached depending on whether the population doubles every six or so years (10% increase) or whether the doubling time approaches infinity (as $\lambda \rightarrow 1.0$).

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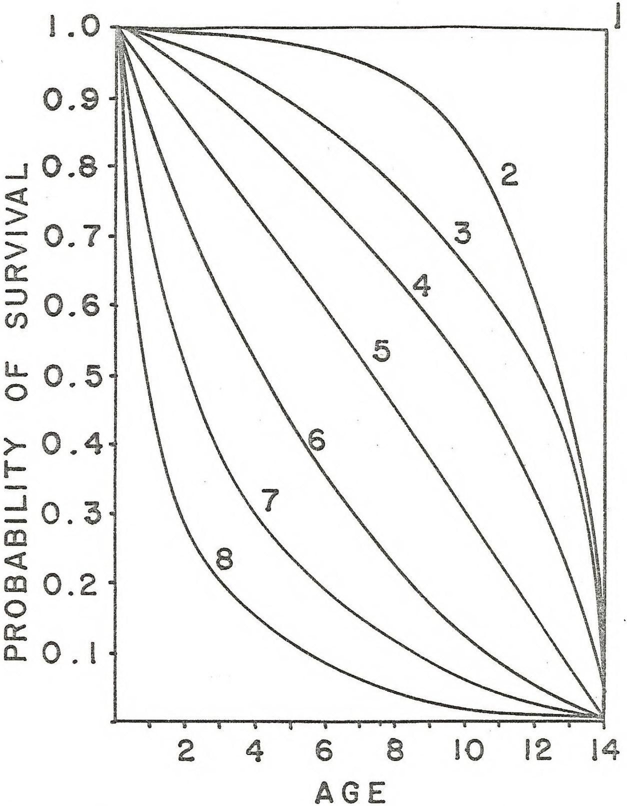

Figure 1. The array of survival schedules across which simulations were conducted. Schedule 1 represents a theoretical maximum; schedule 2 through 8 are simply representative of the variation available.

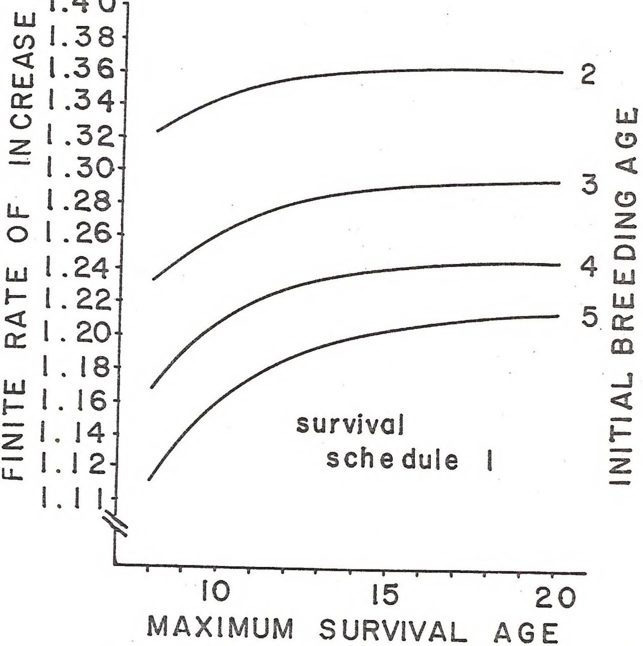

Figure 2. Finite rates of increase (λ) obtained at various maximum ages and at four differing ages at first breeding schedules. Note that these simulations were conducted using the maximum theoretical survival schedule, and 100% breeding across all breeding age females.

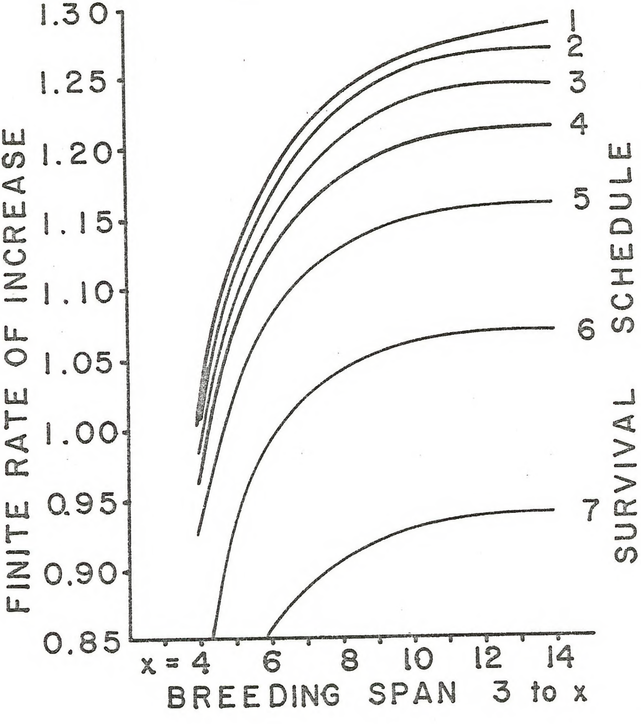

Figure 3. Finite rates of increase (λ) obtained at various durations of breeding participation across survival schedules 1 through 7. Survival schedule 8 is off the graph and thus not presented. These simulations were conducted using 100% breeding across all breeding age categories.

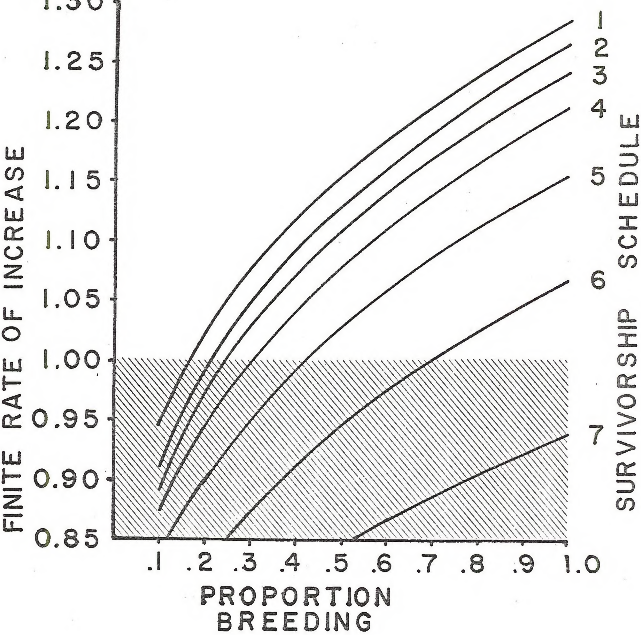

Figure 4. Finite rates of increase (λ) obtained at various proportions breeding across survival schedules. Age at first breeding was three for all simulations, and proportion breeding was constant across breeding ages within simulation sets.

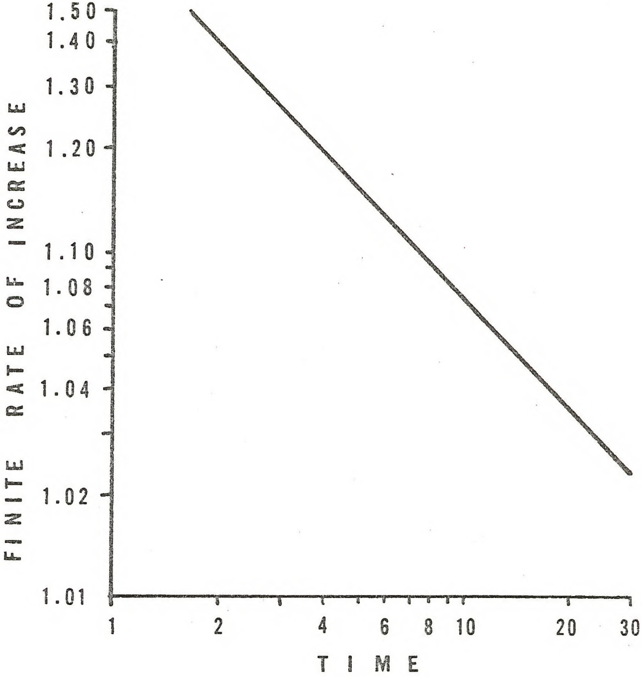

Figure 5. Doubling times resulting from various finite rates of increase. See text for discussion.

Age Structure, Condition, and Reproduction of Two Burro (*Equus asinus*) Populations from Grand Canyon National Park, Arizona

George A. Ruffner and Steven W. Carothers
Harold S. Colton Research Center, Museum of Northern Arizona, Flagstaff

Abstract

Results of an investigation of age structure, condition, and reproduction of two burro (*Equus asinus*) populations in Grand Canyon National Park, Arizona, are presented. Sixty-three animals from two areas were sacrificed and autopsied. Age structure of the two populations was significantly different and the burros in the Bedrock Canyon study area were in better condition than their counterparts in the Lower Canyon. There were no differences in reproduction between the two populations and recruitment rates were similar. Differences in age structure in the two populations may be related to the intensity of past burro management practices in the Bedrock Canyon area. Financial support for this research was provided by a National Park Service Contract (No. CX 821050007) to the Museum of Northern Arizona.

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Ecological Overlap Between Feral Burros and Desert Bighorn: A Literature Review

Rick F. Seegmiller
Department of Range and Wildlife Management, Texas Tech University, Lubbock

Abstract

The feral burro (Equus asinus) roams freely, under stringent federal protection (P. L. 92-195), throughout many desert bighorn (Ovis canadensis mexicana, O. c. nelsoni) ranges in the Southwest. The burro's widespread distribution, increasing numbers, and ecological impacts offer a threat to desert bighorn populations.

This paper reviews and summarizes literature regarding both ecological overlap (habit and dietary) and interspecific interactions between sympatric burros and desert bighorn. These data are interpreted in light of fundamental concepts in interspecific competition theory.

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